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CONTRIBUTIONS TO THE PRINCIPLES OF MORPHOLOGY

CONTRIBUTIONS TO THE PRINCIPLES OF MORPHOLOGY

BY

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FOREWORD

THE subject of this work is the analysis of the principles of a pure science. Morphology has few practical applications except in medicine[1] and psychology,[2] and these are not dealt with here. The aim has been to provide a basis for theoretical discussion of the ordinary laws of structure and development, the enunciation of which are too often left to the whim of the individual. The principles of the mathematical and physical sciences have frequently been discussed and on the whole there is much less disagreement about physical and chemical theories than about biological ones. Yet in that branch of biology which deals with the most concrete of all biological data—anatomy—the theoretical basis seems to have received very little attention. For morphology is merely scientific

[1] Pathology has a morphological foundation. For many pathological states in man reproduce normal conditions in some animals, and are interpreted as reversions. See J. Bland Sutton: *Evolution and Disease*, London, 1890, and E. S. Talbot: *Developmental Pathology, a Study in Degenerative Evolution*, Boston, 1911. Other abnormalities have a definite morphological relation to the normal, a very simple instance being seen in increase in number of parts, e.g., supernumerary limbs (see Bland Sutton, *loc. cit.* and Bateson: *Materials for the Study of Variation*, London, 1894). Moreover, many diseases have an absolutely definite morphological localization in the body. A morbid change on one side is often repeated in exactly the corresponding area on the opposite side, in remarkably exact detail. Such symmetrical diseases are most easily seen in many skin eruptions. There is also a strong tendency for morbid conditions to be reflected on parts that are serially homologous, e.g., hands and feet, elbows and knees, successive vertebræ. See St. George Mivart: *Genesis of Species*, London and New York, 1871 (p. 205 *et seq.* where further bibliography on the subject is cited).

[2] A rational psychology should be correlated with brain structure.

anatomy, and its principles have scarcely received the treatment that their interest and value warrant.

In the following pages, therefore, an attempt has thus been made to examine and analyse the principles of morphology from a critical point of view. The nature of morphological thought is first introduced, but no attempt is made to present historical details which are not necessary to an understanding of the subject. A complete history[1] of morphological ideas would be an extensive undertaking, but would hardly aid the object in view. And in the subsequent presentation of the principles of morphology and their analysis, the enormously detailed field of the application of these principles has been avoided. Possibly this leads to the disadvantages of a somewhat arid treatment, but the attempt to illustrate the principles by showing their applications in the details of structure of plants and animals would divert attention from the points at issue, and render the work less available to non-specialist readers.

[1] For a valuable collection of morphological ideas, historically summarised, see E. S. Russell: *Form and Function—A Contribution to the History of Animal Morphology*, London, 1916. But this author certainly underestimates the contributions of Goethe, and particularly of Haeckel.

INTRODUCTION

The study of anatomy is one of the oldest of human pursuits. Not only did it spring up with the origination of primitive medicine and surgery, but it was associated with the art of killing, whether in war or in sacrificial rites, as well as with the age-old practice of embalming. Sixteen centuries before our era, the Egyptians had recognized a number of internal organs, and had at least begun the study of their topographical relationships. Together with some correct anatomical information, such as, for example, the connection of the blood-vessels with the heart, were held a number of erroneous physiological views, or ideas, which should perhaps be treated as examples of early symbolical thought. Air, for example, was said to be present in some vessels, but no distinction was made between the breath and the soul. In Babylonia and China there are indications of still earlier anatomical enquiries, of a somewhat detailed nature. Thus a clay model of a liver from a Babylonian Temple School[1] and in which over a dozen parts are distinguished, has been dated at about 2000 B.C. Chinese anatomical representations[2] extend back ten centuries earlier, and

[1] J. G. De Lint: *Atlas of the History of Medicine. I.—Anatomy.* Ed. C. Singer, London, 1926.

[2] De Lint *loc cit.*, also A. L. Cleyer: *Specimen medicinae sinicae*, 1682, for further details.

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indicate a minute acquaintance with the vascular system of the living body, together with apparently some very elementary misconceptions as to internal structure. In all these it is necessary, in view of the mythical tendencies of early thought, to consider a symbolical interpretation, as well as a concrete representation of the facts. Even at a much later date anatomical facts were intimately associated with such symbolism (e.g. the mediæval astrological diagrams) just as chemistry existed only in the form of alchemy.

Mere anatomical description, however, began before the time of Aristotle, and if his predecessors of the Hippocratic School were but ill-informed on internal structure, he was followed by workers, especially at Alexandria (300-250 B.C.) who laid the foundation of the anatomical knowledge of the classical and middle ages. Aristotle himself pursued the dissection of animals to a considerable extent, including a number of marine invertebrates in those he examined.[1]

A scientific anatomy begins when the parts of the body are not merely described, but compared and classified, and when explanations of their presence and their characters are attempted. Probably anatomy became scientific at an early stage in history, although like other sciences it appears to have been little developed. Its greatest progress, as a science, resulted from the development of comparative anatomy and embryology, which supplied a wide range of data favourable to the building up of an extensive system

[1] *Historia Animalium.*

of theories and hypotheses, i.e. of a science. Although a unity of plan in diverse organisms was recognized by the Greek philosophers, and some particular instances of it are mentioned by Aristotle, many of the older anatomists seem to have been strangely immune to the idea. The dissection of animals and even of the human body was practised in antiquity, and considerable anatomical knowledge was accumulated in the Middle Ages. Even when other branches of science were at their lowest ebb, public dissections of human and animal bodies were carried out at certain places, and although anatomists were persecuted like other researchers, their activities were never so completely suppressed.[1] Now in spite of all this, the unity of plan was as foreign to mediæval thought as the heliocentric system of astronomy. Even among the Greeks no extensive scientific or philosophical treatment of the subject was made, as far as the writer is aware. Thus the scientific investigation of organic structure is on the whole a more recent development of the subject, contemporaneous with the similar expansion of human interests over many other fields of investigation.

The history of comparative anatomy shows that the perception of the unity of plan became clear to certain anatomists as soon as the observation of the structures themselves was sufficiently advanced. Not all who have studied the variety of animal structure have concerned themselves with anatomical laws of structural plan, but along with the advance in knowledge of

[1] Proof of this will be found in the works of C. Singer.

the bodily construction and peculiarities of animals, which began at the end of the eighteenth century, a knowledge of form relationships began to spring up, depending upon the perception of what was afterwards known as *homology*. The latter term is used for the structural equivalence of organs or organisms. It depends upon the existence of a unity of plan in the organization of two different parts or bodies. To be homologous, however, a differentiation of structure must be present in each, and the relationship of the parts within each must be comparable. The wing of a bird is well known, for example, to correspond in structure with the fore-limb of a mammal. As soon as comparisons of the anatomy of different types of organisms began to be made the unity of plan began to appear clearly. Everyone will admit the fact that the bodies of many animals are built up on the same plan as that of man, and, curiously enough, the older anatomists seemed to have used human and mammalian bodies indiscriminately, e.g. Galen (A.D. 131-201) used monkeys, dogs, pigs and bears. "The internal organs of the pig were thought to correspond fairly closely with those of man."[1] Rufus (A.D. 100) dissected apes. Later differences were observed, and comparative anatomy began.[2] Hieronymus Fabricius

[1] De Lint, *loc. cit.*

[2] Aristotle had compared the upright posture of man with the horizontal position of the quadruped. He had also likened the cephalopod, as its name implies, to a higher animal, the body of which had been folded in two so that the feet arose from the head. Other dim suppositions of form correspondences are traceable to antiquity, but the equivalence in internal structure is relatively much later, as has been seen.

(1537-1619) was essentially a comparative anatomist, noting resemblances and differences between animals. Pierre Belon, about the same time, extended anatomical studies from quadrupeds to birds and fishes. In 1551 he produced a figure showing the skeletons of a man and of a bird side by side for comparison. Giulio Casserio[1] (1561-1616) and Volcher Coiter (1573-1575) also made specific comparisons of different types of animals. Comparative anatomy became definitely established, as by the researches of Eustachius (1520-1574) and Peyer (1653-1712) for example. The unity of plan was clearly recognized in the *Zootomia democritea* of Severino (1645). Formal lectures on the subject were first given[2] by J. F. Blumenbach (1752-1840) at Göttingen.

Thus at the end of the eighteenth century comparative anatomical studies had advanced to a stage which favoured the maturing of synthetic views of organic structure. The emergence of a comparative science of organic form was also stimulated by the development of philosophy at a time when the latter was not segregated from the knowledge of nature. At this time there was no separation of an artificial philosophy of the abstract from an equally artificial empirical science, both of which may be claimed to exist, side by side, but without interaction, at the present day.

The first complete presentation of the idea of a

[1] A very striking comparative diagram by this author showing the ear ossicles of man, calf, horse, dog, hare, cat, mouse, pig and goose is reproduced by Singer. *The Evolution of Anatomy*, London 1925.

[2] De Lint, *loc. cit.*

general view of form, which would not merely place together, but show the dynamic nature of the relationships which subsist between organic constructions, was made by one whose scientific attainments were overshadowed by his literary eminence, but who, in both fields, was equally an exponent of the monistic philosophy. The idea of a science of form that would synthesize all facts of organic structure and development in plants and animals, including man, was developed by Goethe in his *Morphology* of 1817. In 1790 in his *Metamorphosis of Plants* he had proved conclusively that the various appendages of the plant, from cotyledon, through the various types of stem leaves to the appendages of the flower (petals, stamens, etc.) were equivalent. He represented them, therefore, as modifications of a single primitive appendage. This primordial organ was not regarded by Goethe as an idea, but, as proved by his own account[1] of a conversation on the subject with Schiller, was to be considered as a reality. It must not, however, be confused with the "primitive type" of modern evolutionists as hypothecated as actually existing at some time and place and to which we shall have occasion to refer subsequently. It is, on the contrary, something perceived in the plants themselves and the relationships between them.

The subject of the unity of plan was steadily pursued by Goethe. In his time the human skull was regarded as distinct from that of animals in showing no trace of

[1] Goethe: *Conversations with Eckermann.*

the premaxillary bone, a small ledge of bone supporting the two upper incisors in most mammals. By examining a number of skulls he was able to prove that this supposed human distinction was absolutely fictitious. The bone is there and in some cases can be found separate as in animals.[1] The failure to recognize it in normal adult skulls is simply due to its fusion with the adjacent bone.

Another of Goethe's scientific achievements, which is still remembered, is his formulation, independently of Oken, of the vertebral theory of the skull. According to this view which was expounded by Owen and others in later years, the skull itself is a metamorphosed portion of the vertebral column, or more correctly, as Goethe himself expressed it, both skull and column are expressions of the same primitive type.

These are a few examples of Goethe's biological conceptions ; there are many more of them scattered through his voluminous scientific writings.[2] Not only special studies of this kind, however, but his philosophical insight and wide interests led him to the establishment of the comparative science which he called morphology. According to Goethe, all the objects of nature form a connected whole. They are produced by the activity of an internal force, which seems to be equivalent to the *creative energy* of the Greek

[1] It is always separate in the human skull during early stages of development.

[2] Goethe's *Naturwissenschaftliche Schriften, herausgegeben von R. Steiner.* 1883-1897.

philosophers (e.g. the " fire " of Heraklitus),[1] the *lubet* of Boehme and other mystics, and the *libido* or *horme* of modern psychologists.[2] But it must not be associated with animistic, vitalistic or dualistic views. Goethe was a monist, and assimilated the profoundly synthetic philosophy of Spinoza to whom he frequently refers. He believed in the animation of the whole of nature, but not in animism, which separates the soul from the forms of matter. The internal force of nature, he thought, shapes matter as the mind of the artist imparts form to his work. This will only be construed as a dualistic conception by those who are oblivious to his equally important view of art, i.e., that artistic creation is itself a continuation of the development of nature. Like Haeckel who took over the philosophy of Goethe and Spinoza he found the soul in all material objects, never separated from them. Haeckel is generally considered as the typically materialistic philosopher, but he always spoke of monism, and his synthetic views are closely allied to those of Spinoza, Goethe and the philosophers of Nature, and have nothing in common with that physico-chemical materialism which has no place for form and relationship in its concept of nature.

Goethe was a close student of Linnaeus but his attempt must be considered as a reaction to the separative and systematizing tendencies of the Linnaean

[1] E. Pfleiderer: *Die Philosophie des Heraklit von Ephesus* sums up the essential basis of the philosophy of Heraklitus in some verses by Goethe.

[2] C. G. Jung: *Wandlungen und Symbole der Libido*, Zurich. Eng. trans. as *Psychology of the Unconscious*, New York, 1919, London, 1920

school.[1] The study of living things was, among the latter, simply divided in correspondence with Linnaeus' two kingdoms of animate beings, into botany and zoology, branches of study which have survived to this day, like the binary nomenclature for species also established by Linnaeus, for reasons of convenience in practice. But this involves no difference of scientific method in the treatment of these two realms of nature. The method in each case was classification, and even this was admittedly artificial, so that botany and zoology contained, at that time, comparatively little of what can be justly called science. On the other hand Linnaeus and his pupils were succeeded by a school of naturalists who recognized the unity in diverse natural phenomena and even attempted to find philosophical connections between things which are not commonly considered as related. This was the school of the philosophy of nature, of which Schelling and Oken were representatives. Apart from the speculative views of this school, which cannot be dealt with here, a great contribution was made by means of this synthetic method, when an evolutionary conception of species and a natural system of classification began to replace the old and static view of species and the artificial system. The term *biology* was first used as early as 1802 by Treviranus, and, curiously enough, independently, it appears, in the same year by Lamarck, to denote the science of life in its most general aspects.

[1] Goethe gives these particulars himself in the History of his Botanical Studies. See *loc. cit.*

It arose from the recognition of the unity of certain processes of function and evolution in animals and plants. The unity of structure, based on the cell, was already fully recognized about this time, the cellular structure of all organisms, including the unicells, being first definitely formulated by Oken[1] in 1805, although, of course, cells of tissues were known over a hundred years earlier,[2] the well-known cell theory of Schleiden and Schwann proclaiming the identity of cellular structure in the higher animals and plants. The unity of plan, which Goethe attempted to trace, and to place upon a dynamic basis, was thus only one of a number of natural connections which were being investigated during the same period. Many of these belong to the domain of what is now called *physiology*. Biology can be studied both in its *structural* and its *functional* aspects, and it is generally supposed that these two different ways of considering organisms have led to its division into morphology (i.e., scientific anatomy) and physiology (the science of function). But analysis shows, as we shall have occasion to demonstrate subsequently, that these two different aspects of organisms condition two different *scientific methods*, for method is, in actuality, bound up with subject matter. These two methods are, as we shall see, not mutually exclusive. On the other hand, as will appear, they are supplementary. But for this reason itself morphology can never be explained on a physiological basis, nor can

[1] L. Oken: *Die Zeugung*. Frankfurt b. Wesche, 1805.

[2] Malpighi's *Anatomy of Plants*, 1675, was intended to form a basis for the understanding of animal structure.

physiology be reduced to morphology. It is true that Goethe had a wider conception of morphology than that held at the present day, when the subjects of its study are the comparison and relationships of living things[1] and their development. His complete monism enabled him to take into the scheme the forms and transformations of non-living objects, such as rocks and clouds. Geologists sometimes use the term morphology in connection with the physiographical features of the earth's surface,[2] but by this they do not imply any common basis for such forms and the shapes of living things. Goethe also included in his scheme the functional relations of organisms, but the connections he traced were not physico-chemical ones, depending upon cause and effect, as discoverable by the analytical and experimental methods of modern physiology, but rather comparisons or syntheses of the kind so predominant in the speculations of the philosophers of nature.[3] Thus, to take a simple example, he compares the production of honey with pollen formation. For Goethe, morphology was the attempt to understand the whole of visible and tangible nature, not from the modern casual point of view, but by the tracing of relationships by the comparative method. It would appear that the relationship of cause and effect

[1] As the author has previously pointed out, it is quite unnecessary as is so often done, to speak of "comparative" morphology, since however the subject is delimited it implies the comparative method.

[2] The term "morphology of the surface of the earth" was first used by C. F. Neumann, according to Zittel (*Gesch. d. Geologie*, 1899).

[3] Goethe can, in fact, be considered as one of the first of this school, although his writings lack the highly fantastic character of some of the latter. Goethe's views, including his theory of colour, were taken over by Schelling and Hegel.

in its narrow sense is only one of the connections between natural phenomena, and that Goethe opened up a way towards the investigation and differentiation of other types of inter-relationship.[1]

The morphological views of Goethe were not taken up very rapidly. Anatomists of his day even refused to believe in the existence of the human premaxillary bone,[2] notwithstanding the fact that he could have shown them specimens of it. A few workers carried on the study of the unity of plan. To Goethe's conceptions, E. Geoffroy de St. Hilaire[3] added the "principle of connections," viz., that similar parts occupy similar relative positions in all animals. Before Goethe's death there were a number of philosophical workers who put forward similar views, but they met with opposition from the empirical school. With the advent of Darwinism, the subject received an enormous impetus. Darwin says of morphology[4] : "This is one of the most interesting departments of natural history, and may almost be said to be its very soul." Darwin, however, did not by any means make use of the anatomical evidence of evolution to its full extent. This was left for Huxley, and particularly for Haeckel,

[1] Haeckel's views of phylogenesis (the development of the race) as the cause of ontogenesis (the development of the individual) is an example of such an inter-relationship, the term cause not being usually used for such relationships. Nevertheless, although his terminology is liable to misunderstanding, Haeckel has therein indicated the essential unity of these different types of inter-relationship.

[2] G. H. Lewes. *Life of Goethe,* with introduction by Havelock Ellis, London, 1908.

[3] E. Geoffroy de St. Hilaire : *Philosophie anatomique I.,* Paris, 1818.

[4] C. Darwin : *The Origin of Species by Means of Natural Selection.* London, 1859. (Sixth Edn., 1872).

who combined a profound knowledge of comparative anatomy with a synthetic manner of thought.

Thus morphology began as a kind of nature philosophy, attempting to trace connections between diverse natural objects, and later became absorbed in evolutionary biology, of which it forms the basis. In a general philosophy of nature, all sorts of connections may be traced, some being mere comparisons, others relations of cause and effect. The causal relations have chiefly been worked out in the realm of physics and chemistry. Nevertheless in Goethe's morphology, and the subsequent evolutionary thought, a mere comparison of forms is insufficient. We have seen that homology is something more than the mere possibility of placing forms side by side. It involves a positive similarity of plan, actually expressed by the organism and perceived by the observer. But even in its beginnings morphology involved something more than the relationship of homology, since there is a kind of seriation of homologies which is now expressed in the evolutionary series. Goethe recognized this, and spoke of the process by which organisms or parts of organisms are related by the name of *metamorphosis*.[1] This pervaded all structure, according to his view, so that he preferred to speak of formations (*Bildungen*) and transformations (*Umbildungen*) rather than of forms (*Gestalten*). He recognized even a sense of direction

[1] Goethe: *Versuch die metamorphose der Pflanzen zu erklären*, Gotha, 1790. This article has been translated into English and published (with notes by M. T. Masters) in Seeman's Journal of Botany, Vol. I., 1863.

in which this metamorphosis took place. Thus the primitive organ of the plant shows three kinds of metamorphoses which he called regular, irregular and accidental. Regular metamorphosis, for example, which may also be styled progressive, is seen in the ordinary development of the plant, the primitive organ successively expressing itself in the seed-leaves, stem-leaves, bracts, calyx, corolla, stamens, pistil and fruit, the transitional nature of the various members of the series being fully recognizable. But the plant as a whole is only a succession of individual members, which are differentiated among themselves. He considered the individual, whether animal or plant, to be composed of subordinate individuals, a fundamental morphological condition which was subsequently examined in detail by Haeckel,[1] and which, as it appears in plants, has formed the basis of the various types of phyton-theory.[2] Goethe expressed his view of the organism in the clearest terms. The living thing is not a unity but a plurality.[3] The existence of these subordinate units (*phyta*, *metameres*, *antimeres*, etc.) is a fact, not a theory. But these units are sometimes differentiated among themselves and subordinated to one another, and the degree of dissimilarity

[1] E. Haeckel: *Generelle Morphologie*, Berlin, 1866, partly reprinted as *Prinzipien der Generellen Morphologie der Organismen*, Berlin, 1906.

[2] Any observer looking at the branch of a plant can see the repetition of nodes bearing leaves, although the first clear perception of this fact may have required considerable insight. Experiments with students show how extraordinarily difficult it is for those trained in causal ways of thinking to detect such relations without help. Yet the resemblance of a branch to a complete tree was pointed out by Hippocrates in *De Natura Pueri*.

[3] *Zur Naturwissenschaft überhaupt, besonders zur Morphologie*, Stuttgart and Tübingen, 1817.

and division of labour is a measure of the grade of organization of the organism. Thus not only are the component units considered as stages in a metamorphosis, but organisms as a whole must be arranged as stages of a greater metamorphosis. Just as there is a primitive leaf segment from which all the segments of the plant are derived, so there is a primitive plant type (*Urpflanze*) of which the individual species are representatives. The composition of the animal organism was chiefly studied by Goethe from an osteological point of view, but this forms a natural basis for the consideration of the whole organism. The vertebra with its ribs and other appendages constitutes a unit in the same manner as the stem node and its attached leaf. These segments of the plant or animal show the same unity of plan as do the individuals of the same class. Thus Goethe says they are alike in origin, but may be either alike, or different in appearance.[1]

Goethe thus held a pluralistic view of the organism, such as is expressed in modern phytonic and metameric theories, but by pointing out the differences, as well as the resemblances, of the segments, he afforded a basis for the unity and individuality of the whole. For it is the differences, subsumed under the anthropomorphic guise of " division of labour," which form such a well-recognized principle of biology. It is they that constitute the unity of the individual as a whole and are the basis of the *organismal* conception of the individual. But the differentiation of parts, while supplying the

[1] *loc. cit.*

principle of *organic unity*, also supplies the basis of *individuality*, by means of the possibilities of variation afforded between the different associations which make up the individuals.

It was the dynamic element in Goethe's morphology which led to its importance in the Darwinian epoch. This is clearly expressed in his definition of the different kind of metamorphosis. It is exhibited in another aspect in his view of the expansion and contraction of organs, which expresses, in a perfectly natural manner, the fact that homologous organs may be of varying degrees of development, some being large and elaborate (expanded) like the green leaves of the stem, others small and simple in structure (contracted), or as we now say vestigial, as scale leaves. In some ways Goethe's terminology is more satisfactory than the modern, as it keeps closer to nature.

It will be impossible to trace all the developments of morphological observation and thought. In botany August St. Hilaire carried the view of metamorphosis to a higher development, distinguishing various methods by which changes of structure come about. Owen, in zoology, elaborated the *archetype*, which is, of course, nothing else than Goethe's primitive type. Correspondence of form, leading to the dynamic idea of metamorphosis, was thus clearly recognized before relationship by descent was clearly formulated.[1]

Even developmental comparisons were made before the Darwinian period. Swammerdam in his *Bibel der*

[1] See Crow: *Phylogeny and the Natural System*. Journ. Genetics, 1926.

Natur, 1785, had compared the life-history of man, frog and insect. But following the clear evolutionary views of Lamarck and Darwin, the developmental comparisons, as well as those of adult structure, were fully recognized.

In order to understand the development of morphology in the post-Darwinian epoch, let us turn our attention to the conception of homology with which we started and which we have seen was so clearly enunciated by Goethe.

In 1843 Owen distinguished between two kinds of resemblance which he called *homology* and *analogy* and this nomenclature has been accepted by zoologists. The distinction between these two conditions rests solely on anatomical comparison and can only become clear by perception of the actual anatomical plan. Thus resemblance in function and appearance often leads us to give the same name to structures which are essentially different in structure. This is what is called *analogy*. Insects and birds both have wings, for example, but there is not the remotest anatomical resemblance between the two structures. The resemblance in body form between whales and fishes is another well-known instance of analogy. Even Linnaeus at first made the mistake of placing whales with fishes, and there are a number of superficial characters in which they resemble one another. Why, then, do zoologists place whales with the mammals, neglecting their marine habits and apparent similarity with fishes ? The answer to this question is of the utmost theoretical

significance, as I hope to show. The whales are mammals because they conform to the mammalian scheme of anatomy. This scheme has been abstracted by the study of a large number of different species, all of which are placed together in the system of classification because they happen to have it. In other words, whales and other beasts have mammalian characters, e.g., there are seven cervical vertebræ. But why are these particular characters used in classification and not others, such as superficial appearance? The answer is again extremely significant. Simply because these characters are such as have been found by long experience to give a harmonious scheme and bring together organisms which are alike, as it were, to the core. Artificial arrangements have been tried again and again, only to be abandoned because they do not give a coherent system.

It was facts of this kind which led up to the theory of evolution and its acceptance by biologists. Homology was then considered as the criterion of blood relationship. Haeckel and Gegenbaur, for instance, stated quite definitely that evolutionary relationship can be traced by the study of homology, the latter author adding that our knowledge of blood-relationship is directly proportional to the certainty with which homology has been established in any particular case.

The particular working out of unity of plan, and therefore of genetic relationship, was made by Haeckel in his *General Morphology*. This work met with a very cool reception amongst empirical anatomists, in spite

of the fact that most of the ideas with which modern morphologists have to deal are clearly enunciated therein. His *General Phylogeny* was an attempt to work out the complete evolutionary relationships of living things.

Haeckel elaborated the view that there is not only correspondence between adult structures but that also the various stages of development have a correspondence. A simple instance is furnished in the life history of insects. The series in its simplest form is egg—larva—cocoon—imago. The most close homology will only be established between related species if we compare the larva of one species with the corresponding phase of another species. Or take the life history of the frog. A legitimate comparison between fish and frog would compare the tadpole with the fish as the latter shows no metamorphosis in the individual life history.

Amongst an infinite variety of fertile ideas Haeckel enunciated his well-known Biogenetic Law, which states that the life history of the individual is a condensed and modified recapitulation of the evolution of the whole race of animals out of which it has arisen. Previous workers, such as Von Baer, had noted a parallel between the series of stages of development of the individual and the systematic series, but Haeckel was the first to give it definite evolutionary significance and to illustrate its application by an immense wealth of facts, such as for example that the human fœtus at one stage of its existence, has a tail, in a general way,

like that of the adult monkey. The law depends upon anatomical comparison just as homology does : in fact, it may be looked upon as only a very peculiar case of homology, i.e., the correspondence between the series of stages in the life history and the phylogenetic series.

Many adverse criticisms have been levelled at this law. It is repeatedly pointed out that the fœtus does not resemble a monkey, and in a great many ways they are totally different. Nevertheless the resemblances are there and can be seen, and have equal claim to recognition as the differences. How far they can receive an evolutionary application will be dealt with in conjunction with the general problem of interpreting morphological relations in terms of descent.

Morphology thus introduces a number of general principles, which will be discussed in the following chapters. The manner in which these principles are expressed in nature is, however, so vast a field, that an attempt to deal with it here would only confuse these important general issues. It will be necessary to discuss *individuality*, in the biological sense, as it has been defined here. The comparison of individuals and of parts leads to a consideration of *homology*, the principle of the unity of type. The relation of parts will lead to a brief consideration of *symmetry and proportion*. In following the differentiation of individuals the questions of *classification and type* will be considered. The dynamic nature of organic *relationships*, which led to the concept of *evolution* will finally necessitate an account of relationship as a measure of *common descent*.

OBSERVATION AND THEORY

According to current ideas, implied in ordinary language, scientific investigation consists in the *observation* of certain facts, the detection of certain regularities or *laws* ruling or appearing to rule these facts, and the building up from these laws of certain *theories* or *hypotheses*, which are said to *explain* the facts. The collection of explanations relating to any particular set of phenomena constitutes a *science*. Thus science, because it has a certain inherent manner of working, constitutes an orderly arrangement of knowledge, and contains certain principles, such as those of logic, which are never transgressed.

For an account of the various methods of science reference may be made to the work of A. Wolf.[1] From this it will appear that the logical procedures utilized in the different branches of science are not all alike, and whilst several different types of *scientific method* have been particularly applied in the physical sciences, others, such as the comparative and evolutionary methods have met with wide recognition in biology. From the preceding chapter it becomes clear that morphology, in particular, is based on the method of comparison, and that Goethe applied this method over a wide field.

[1] A. Wolf. *Essentials of Scientific Method.* 2nd Edition, London, 1927.

In addition to this, the school of thought, to which Goethe, Oken and Schelling belonged, represented logical procedure in a manner which appears unusual to the modern student of scientific method, but which, on examination, proves to be well founded.

In spite of the supposed extravagancies of the school of the nature philosophy, it cannot be denied that human science is in reality an outgrowth of nature, as they were the first to maintain. Many systems of philosophy hold that in observation the human subject comes into direct contact with external reality and this is certainly assumed by modern science. But philosophers who insist upon the reality of observed fact are inclined to regard theory as something altogether different from observation. In morphology, however, it can be seen that theory is not an altogether different field from observation. When one compares one species with another one may be making a direct observation. The simplest observation is not pure sensation, it is perception.

For example, the sensation of redness by itself, is never actually experienced. What actually happens is that we see a definite red spot at a definite time and place. We also note the similarity and difference between this particular sense experience and other previous ones, the whole process being as involuntary and automatic as the sensation itself. If attention is focused upon an object, as occurs in scientific investigation, the impression not only presents itself more vividly to consciousness, but the perception of the

object becomes more definite in its relations to other objects in space, time, and by similarity. Consciousness, in fact, consists in an orderly arrangement of sensations. In some respects it may be impossible to perceive order, but the existence of the qualities time, space and resemblance indicate a fundamental arrangement inherent in all sense experience. Kant put the same matter in a somewhat different manner. According to his terminology spatial and temporal qualities are imparted to crude sensation as it enters consciousness. Space and time are on this view conditions of awareness, having no independent existence. It is true that spatial and temporal qualities have no significance without their material content, but space and time have as much, or as little, objective reality as sensation itself. Nor can one regard these "forms of experience" as playing an active part in the arrangement of sensation. The latter enters consciousness in a pre-arranged form, and we can equally assume time and space to be products of the human mind as assume sensation itself to be purely psychological activity. Hence, in what follows, form, whether it be an arrangement in space or sequence in time, will be considered on exactly the same basis as those elements of experience which are usually considered as purely sensory, e.g., colour. In fact, it will become convenient, following modern sense physiology, to imagine a sensation of time and of space,[1] which can be measured

[1] See Mach, *Analysis of the Sensations*. English translation, London, 1910.

in just the same way as other sense elements. But if form is bound up with sensation, so is the quality of similarity, which is the basis of the comparison of forms except in their spatial and temporal relations.

In some branches of science the idea of cause and effect predominates. These are the sciences which have, particularly, built up a series of theoretical constructs upon a mathematical basis. The fact that conditions regarded as cause and effect are related in nature, as well as in the subject, is overlooked. As will be maintained in the next chapter cause and effect are relationships of conditions, just as homology is.

It was maintained by Goethe that the process of artistic creation is a continuation of the evolutionary development of nature. This appears to be in harmony with much that has been written on æsthetics, which is outside the scope of this work. It suffices to indicate that art itself has a structure,[1] and that a morphology of the objects of art is not an impossibility. And if art is treated teleologically, as it usually is, its manifestation being referred to a psychological basis or tendency, the latter must itself have an inherent structure or rhythm, comparable with, but distinguishable from the logical dialectic.

The human mind has had a long evolutionary history. It is almost impossible to avoid comparing it with the body. The latter, as represented in man, is only one example of a particular type, the primate. This type has, in its turn, its place in the mammals

[1] See Chapter on Symmetry and Proportion.

and so on. Throughout the great phylum of the vertebrates the same organs are constantly recurring in varying form. Some features of bodily construction, such as that of cellular structure, are common to almost all living organisms. The mind has an enormous number of connecting links with the body, and it is inconceivable, that its structure is not only vastly complicated, but that it is also a reflexion of the still greater system of nature, having itself an orderly, although infinitely complex organization. And this holds good whatever view one takes of the relation of body and mind. Not only the human body, but also the human mind, are only examples of matter and mind in general, whatever these two categories may be resolvable into. Hence a theory which cannot fit the human mind into its place in nature, as well as showing how the mind reacts to nature, is undoubtedly inadequate. Hypothesis and theory represents nature, but only because it is itself an outgrowth of nature, and, like a resonator, gives forth the note to which it is tuned.

INDIVIDUALITY

Living things present themselves to us in the form of individuals. The concept of an individual is undoubtedly one needing analysis, and certainly contains a strong anthropomorphic element. In the earliest forms of thought of which we have record the human individuality was projected everywhere into nature. This kind of animism has not disappeared from thought ; one finds traces of it in various systems of philosophy at the present day. What relation the human being bears to the inorganic world in such schemes is somewhat difficult to ascertain. On the other hand, orthodox biology holds that it is legitimate to compare the body of man with that of the higher animals and, as man is still regarded as an individual, zoology has not yet shaken off the idea of individuality in animals. Yet although this concept is deeply rooted in biological literature, it is somewhat remarkable that the subject of individuality has received so little attention from biologists, many of whom seem to be unaware of the importance of differentiating this concept. If it were possible to ignore the question of individuality, as in physics, the terms might be dismissed as having no scientific meaning whatever. Unfortunately, as we have shown, the data of biology are of such a nature that the individual cannot be

disregarded. It is as much a fact of observation, i.e., a sense perception, that life appears in the form of individuals as that these units have a definite size and shape. Hence the necessity for a science of individuality, just as the observation of colour involves a science of light.

The general tendency to formulate theories on the model of physical theories, and the inability to treat individuality in this manner may be partly responsible for the neglect of the study of this subject. It must be emphasized that with a different type of data the method of science becomes different. Individuality as a concept undoubtedly contains a strong anthropomorphic element, but it must be remembered that the human subject is a true example of the individual and hence the idea of the latter must always contain an element of anthropomorphism. The idea of individuality will, for example, be more obviously anthropomorphic than the ideas of physics. Yet even the idea of energy, which dominates physics, can never be completely freed from an anthropomorphism. As A. Wolf[1] has said—" Language is the creation of man, and the tendency to anthropomorphism is its original sin. If science is to avoid every suggestion of anthropomorphism it must be dumb."

Correlation of Parts.

The individual, however, can be defined without recourse to the ordinary ideas of teleology. In all

[1] *Essentials of Scientific Method.* London, 1925.

individuals as ordinarily understood, there is a certain correlation between the parts which does not exist in the non-living object. It will not be necessary to deal here with the different kinds of individuals and with the difficulty of defining the individual amongst the lower organisms, because this is a special problem of homology. The limitations of individuality were dealt with by Herbert Spencer[1] and Haeckel.[2] Attention will be confined to the typical individual unit, such as the human body. This obviously has the property of isolation, since it is on the whole quite easy to distinguish, at any one moment, what belongs to the individual and what is external to it, i.e., belongs to the environment in the wide sense. If such an isolated unit be compared with the apparently isolated units of non-living portion of matter occurring in nature it can equally well be separable from the rest of nature by its physico-chemical properties. A crystal is an example of this, and is usually instanced as the typical inorganic individual. A chemist would say that the crystal was composed of molecules, a physicist might consider it as made up of atoms or even electrons. But there would be no correlation between these units, or any other subdivisions of the crystal, of such a nature that knowledge of the one part would suggest the existence of another. Yet this is precisely what occurs in living individuals. The structure of a limb instantly suggests a body to which this limb was attached. And this is not only

[1] *Principles of Biology*. Vol. I., London, 1884.
[2] *Generelle Morphologie*, Berlin. Partly reprinted as *Prinzipien der generellen Morphologie der Organismen*, Berlin, 1906.

because by constant association of limb and body we have come to regard the two as inseparable, merely by association of ideas. We do not regard the density of a given substance, such as lead, to be great, simply because we have always associated the look of the substance with the high specific gravity. The structure of a limb is unintelligible without the structure of the body. The complication of the human brain would be impossible of interpretation were it not for a knowledge of its connection with the other body tissues via the nerves. There is something in the form or structure in any part of an individual which implies the existence or at least the possibility of other parts.[1]

Simultaneous and Successive Inter-relations.

Here it should be noted that there is not only a relation between different parts that are co-existent, but that there is a time relation, so that the parts only have a definite significance in relation to the whole life of the organism. For example one may note a plant with a thick underground stem. The thick stem is without full significance for the plant as it exists at the present moment. It is only when one considers the whole individual life history that one sees the meaning of the thick stem in relation to the whole. The plant is frequently described as showing food storage.

The illustration given here may seem to be of physiological rather than morphological interest.

[1] This definition of the individual is quite in harmony with the views on individuality given by J. S. Huxley (*The Individual in the Animal Kingdom*, London, 1912.) Other attempts to define the individual are discussed by this author.

Teleological explanations of structure usually translate the explanation into functional terms owing to the very anthropomorphic nature of teleological explanations as generally used. Ordinary explanations of such phenomena, e.g., of storage organs are based on the comparison of the *development* of a plant or animal with the *behaviour* of a human being. Of course this may not be justifiable. But an explanation of structure existing at any given moment in terms of a future structure may nevertheless be legitimate, although available terminology is not well adapted to describing this fact without using the human consciousness of purpose as an analogy. It is very difficult to explain the reproductive organs, for example, as not having an aim —i.e., the production of a new generation and this is because they bear a definite relation, comparable with the causal relation, but reversed. In reality both causality and teleology are two methods of description, both of which are anthropomorphic representations of the actually observed relations within the organism.[1] These relations can be best termed the individuality of the organism.

The illustration of food storage illustrates a morphological principle. If the structure of the alimentary canal is not thoroughly understood, it is futile to attempt to study nutrition. It is often said that function precedes structure. This is one of those dangerous half-

[1] I am informed by Prof. Wolf that the view of teleology taken here has been put forward and elaborated by L. T. Hobhouse in his *Development and Purpose*. It will be unnecessary to discuss it more fully, however, as it is merely used in the service of scientific method.

truths that can be used to "prove" many favourite hypotheses. In fact function and structure must change at the same time, because difference in function involves difference in structure. The truth of the statement, which is not usually made obvious, is that functional changes can often be detected before measurable structural changes have come about. Thus a functional difference may be observed between the apparently similar cells (isogametes) of two conjugating *Spirogyra* filaments, but it is impossible to believe that no minute structural difference exists. Even during sleep histological changes take place in the nerve cells.[1] It may be conceived that these differences are only chemical ones. But to this it must be replied that all structural changes are physico-chemical ones. The formation of a new cell is nothing more or less than the increase of different amounts of chemical substances and changes in their states of aggregation at certain points, and the growth of the cell is the prototype of all growth.

The description of storage in the plant which we take as an example thus involves a teleological mode of expression, and although the majority of biologists are opposed to teleology as theory, they are continually finding themselves using terminology having teleological implications. The very fact that this is so is an indication of the existence of organic individuality as something distinct from the phenomena of physics and

[1] See L. Errera: "*Pourquoi dormons-nous?*" Bull. Soc. Anthropol. Bruxelles, 5, 1886-7, repr. in *Revue scientifique* 1889, and in *Recueil Inst. Bot. Brux.*, 4, 1920.

chemistry. In the physical sciences, teleological explanation is not now found convenient. Possibly there is no fundamental difference between the facts of biology and physics in this respect, however, and even a teleological mode of expression might be adapted to the non-living and was in fact used in mediæval times by the alchemists, in dealing with non-vital phenomena. It is possible that the anthropomorphic element which renders teleology so objectionable might be eliminated. The actual fact of adaptation towards future conditions cannot be denied, although natural selection may be considered as sufficient to account for this adaptation. Thus an organism has had to adapt in some way, e.g., to store food, in order to survive. Possibly the very fact of organic individuality was forced on matter by natural selection as soon as it became capable of reproduction, the lowest grades of organisms showing the least defined individuality. In any case it seems better to include individuality as a special case of the general law which includes also the relation of cause and effect. For in the organic individual, the existence of the one part implies the other. This is shown by those experiments in embryology in which a small special part of an embryo is made to reproduce the whole organism, as well as in all the numerous facts of ordinary regeneration. The whole of experimental embryology shows that there is a principle of symmetry or balance between the different parts, and the growth of distorted into normal embryos seems impossible to explain without this principle. The latter

is reduced by the mechanist school, of which Jacques Loeb is the best known exponent, to an arrangement of chemical substances, whilst according to the vitalistic views of H. Driesch and others a super-mechanical entity comes into play. It is sufficient here, however, to point to the existence of a form of organization which—although it may be "explained" in physico-chemical terms—is actually somewhat special and confined to living things. This form, organization or arrangement constitutes the individual.

Having already referred to the time relation, whereby a part or organ at one stage bears a relation to the complete arrangement in time called the life history, it becomes clear that certain parts, viz., those responsible for producing a new generation, are related to a new set of parts which make up the new organism, more obviously than to the parts of the parent body. As, however, the parent itself must have had an origin, this makes no difference to the general arrangement which constitutes the individuality. The problem of actually defining the individual in any given case is one of homology, and it makes no difference whether we consider the individual as beginning with the fertilized egg, or at some other point, provided the individuals present a rhythmic sequence. The quality of differentiation is the principle on which the individual is based, but this is not haphazard or arbitrary differentiation. The parts must occupy certain positions with reference to the whole, if the individuality is to be maintained. The possibility of

an artificial interference with the arrangement or even sometimes a natural occurrence of new arrangements is not thereby excluded. Even abnormalities have a definite structure or arrangement, and are frequently of the highest morphological value in showing the relationships of the species in which they occur.[1] There is a law in the abnormal, as well as in the normal.

It has now been shown that individuality can be linked up with the laws of cause and effect as they act in the purely mechanical realm. For the reasons which will now be given, however, it will be advisable ot maintain that individuality is a principle underlying all structure and development, rather than to reduce the latter phenomena to the mere workings of physico-chemical laws. There are other features of the individual which must be described, and for which these laws are inadequate, although this does not mean that there is at any point a contradiction of the laws. It might at first be supposed if we consider the individual life cycle as a series of events which we may symbolize as *a*, *b*, *c*, *d*, *e*, then *b* is the result of all the forces which have acted on and from *a*, whilst in a similar manner *c* follows from *b* and so on. This is perfectly justifiable. But in many actual cases the condition *c* is the more obvious explanation of *d* than *vice versa*. This is the ordinary teleological explanation, already illustrated by the case of the plant having a thick underground stem. The condition of the stem is " explained " as a storage which enables the flower to develop at a later

[1] See e.g., Wordsdell: *Principles of Plant Teratology*. 2 vols. London, 1915-16.

stage. Many embryonic appearances in animals can thus best be interpreted as structures which to use the ordinary evolutionary terminology, have receded, during the evolutionary history from the adult stage into the embryonic phases of the life history.[1] In other words, it is just as easy to conceive the adult as being the cause of the embryo as the embryo of the adult, although most of us favour the latter way of thinking as being capable of being brought into line with the ordinary laws of physics and chemistry. The vitalists and teleologists have, however, been led away by the opposite view.

The structure of an organism at any given moment can also be symbolized by the series *a*, *b*, *c*, *d*, *e*, where each letter represents a part or organ. Two very well-known views have contested for supremacy with regard to the relation of the parts to one another. As is usual where two views have long held ground in science, they each represent a partial account of the situation. According to the hypothesis of epigenesis the parts *a*, *b*, *c*, *d*, *e*, owe their differentiation to the action of one another, so that *a* is the cause of *b*, *b* the cause of *c* and so on, it being left undecided whether *b* might not also be the cause of *a*. This view has gained ground during the epoch of experimental morphology, because in many cases different isolated parts of the adult, e.g., *a* or *b* can be made to produce the rest of the organism *bcde* or *acde*, making it unnecessary to assume with Weismann the segregation of a distinct germ plasm,

[1] For numerous examples of these, see L. S. Berg's *Nomogenesis*, English translation, London, 1926.

which was preserved from differentiation and stored up alongside the differentiated parts *abcde*. Thus the adult leaf of a *Begonia*, or even a small part thereof, may be the actual physical " cause " of the whole plant, just as any seed or embryo may be the cause of the adult. With increasing differentiation in organs or organisms the power of regeneration becomes more and more limited, and hence the opposite view of the cause of differentiation still remains in vogue. This is the hypothesis of preformation, which announces that, in the symbolism used above, *a*, *b*, *c*, *d*, *e*, are not the cause of one another but are due to a preceding stage—something of their structure being represented in the early stage *x*. Thus as *x* is obviously very different from *abcde* an attempt must be made to find some correspondence between the two phases. As *x* is relatively minute, the preformed units will be submicroscopic, the micellae of Nägeli, the physiological units of Herbert Spencer, the plastidules of Haeckel, the biogens of Verworn, the pangenes of Darwin and De Vries and the genes of the modern Mendelians. Some of these have been made to perform nutritive functions as well as reproductive, as at microscopic dimensions the two processes are identical. The arguments for epigenesis and for preformation are equally convincing and it is only by accepting the complete system of relationship described here as individuality, that the observed facts of structure and development can be adequately represented.

HOMOLOGY

Unity of Plan.

Having described under the name of *individuality* the nature of the relation or form which is inherent in each organism, the equivalence of the different organisms to one another must now be considered. But this comparison of different individuals is a process not different in method from the attempt to find what is equivalent in different parts of one and the same organism, or even the comparison of a part of an individual with the whole. In short one is led to the consideration of all the different kinds of resemblance which can be traced among living things, and taking into account what has been said as to the method of the physical sciences, to resemblances among all natural objects.

A certain unity of organization is readily perceived if one examines, for instance, the skeleton of a man and of a horse set up side by side in one of our museums,or still more, by comparing, let it be supposed, a human skeleton with that of a number of familiar animals, say of a cat, a dog, a rabbit, a horse, a pig. The complete anatomical construction of each of these animals might be used as an example, but it is recognized, even by those who have not dissected animals, in the easily handled and familiar hard parts, the bones. The effect which the combined examination of these different

objects will have upon the observer, however, as the writer has ascertained from experience with students first introduced to the situation, will vary. Although the similarity of plan will hardly be denied in such a simple case as that given, yet some will at first see nothing in common between these different skeletons, others will say that they are all alike, pointing out that each consists of a skull, a backbone, ribs, limbs, and so on. In the history of anatomy one finds the same thing. Some old dissectors could see nothing in common between the bodies of different animals, others supposed that they had only to dissect pigs and cats in order to discover the whole of human structure.[1] Because they had no view-point, such as is afforded by the conception of the unity of type, their anatomical descriptions were often an extraordinary mixture of human and non-human structure. Later in anatomical history the problem of the unity of type became clear and, as we have seen, led to the formulation of the science of morphology. Later, when the comparative data were taken over in the services of the evolutionists, this unity became a familiar theme amongst biologists. But it by no means won the same universal assent which the new physical theories of the nineteenth century obtained. A great task of the upholders of evolution, such as Huxley and Romanes, was to draw attention to the existence of the unity in sufficiently diverse types

[1] According to Singer (*The Evolution of Anatomy*. London, 1925) Vesalius was the first to distinguish clearly between human and animal structure, and to point out that the anatomical accounts of Galen were based on various animals other than man.

even to provide a basis for their evolutionary conclusions. Their difficulty was not so much in proving their conclusions, as in spreading a knowledge of the data on which they were based.

If one considers the bones of the arm of a man and of a monkey it is easy enough to see the resemblance and difficult to find differences. If one then examines the bones of the fore limb in a horse the general impression of resemblance is strong, but differences are easily noted in the part corresponding with the finger bones. At first sight the distal end of the limb, with its hoof, is utterly unlike anything in the hand of man or monkey. Yet detailed investigation shows that each bone of the horse's fore limb can be compared with one bone of the human upper extremity. And in this task we are considerably helped by a number of intermediate stages which happen to be fossils.

This homology of parts extends over a very wide field. Thus not only do the upper limbs of man correspond with the fore limbs of other mammals, but they are also homologous with the wings of birds. Belon's diagram set forth in 1555 showing the correspondence between the avian skeleton and that of man has already been referred to. Since his time it has been taken for granted that birds are modified quadrupeds. A confirmation of this view was found in the study of the development of the curious bird known as the hoatzin, stinking pheasant or *Opisthocomus*. This is a wild ally of the game birds and poultry, inhabiting richly wooded lagoons, creeks and rivers of the Amazon

valley. Strictly confined to a life in trees, the young emerges from the egg in an active state and immediately commences to climb. For this purpose it uses not only its enormous feet and its beak, but also its wings which are provided with two large claws. In other words the wings at this stage are still partly feet. The claws disappear in the course of a few weeks and flight takes the place of climbing.

Although confirmations of this startling kind are continually met with by the comparative anatomist, from the point of view of scientific method it must be remembered that the unity of plan is itself the central and fundamental fact, established by sense perception itself, and independent of all accessory considerations. Even if two species alone showed the actual, visible and tangible resemblance, the relation between the two would be sufficiently established. The existence of a third form, intermediate between the first two, greatly strengthens the tie, but is by no means essential to the connection. In actual fact the unity of plan can often be traced throughout many thousands of different species.

It is generally admitted, for example, that the quadrupedal plan extends over nearly the whole series of the backboned animals, the four limbs of land animals being equivalent to the lateral fins of fishes. The presence of a backbone and ribs is also characteristic of the vertebrates, in spite of the many modifications to which they are subjected. The same unity of plan can be traced in the circulatory, nervous and other

systems of vertebrates, and it becomes equally clear throughout large series of invertebrate animals. The term *phylum* was used for such a series by Haeckel,[1] and is now accepted by zoologists as the systematic group of the highest order, the widest and most inclusive of all subdivisions of the animal kingdom. Haeckel considered the phylum as a group of species descended from one great common stem, but such series were known before evolution was properly recognized as a principle and were even propounded by authors who unheld the fixity of species. Thus Haeckel mentions as phyla the four types of Cuvier : the Vertebrates, the Articulates, the Molluscs and the Radiates. These were founded by Cuvier on the unity of plan discoverable throughout each series, as the Radiates on their centric organization. Yet Cuvier strongly opposed the principle of evolution, upheld by his collaborator and rival, Geoffroy St. Hilaire.

Whether these phyla exhaust the possibilities of the finding of unity of plan does not affect the actual perception of that unity within the phylum. Both plants and animals can be divided up into such main groups, and generally they consist of many thousands of different species. In other words the unity extends over a wide field. Only in a few cases is it necessary to set up a phylum for a very narrow range of species, e.g., plants of the *Chara*-type, because they are widely separated from all other organisms.

Unity of plan in such large series is sometimes

[1] *Anthropogenie*, English trans. as *The Evolution of Man*, Lond. 1910.

combined, one finds, with great diversity. But it is always perceptible as a resemblance. In some cases authors have reduced the unity to a tendency only,[1] and it is quite certain that extremely divergent members of the same phylum would not be recognized as such if the intermediate types were unknown. A tendency cannot be recognized without being founded on some perceptual resemblance even if the latter must be highly analysed by a process of abstraction before such can be recognized.

Within the phylum subsidiary unities can be very readily recognized, and there in turn give place to the unities among still smaller groups which are even more closely related. It is this fact that makes possible and even inevitable *the natural system* with its hierarchical arrangement of sub-groups within the phylum. Homology between closely related species becomes more intensely perceived.

The extent over which unity of organic construction can be traced must be settled by observation and analysis of observation. The older morphologists, such as Goethe and Geoffroy St. Hilaire upheld the unity of all animals and sought to trace a fundamental arrangement throughout all animal bodies. Goethe equally concerned himself with the fundamental plan of the plant. The conclusions of Geoffroy and somewhat similar schemes of Oken and the school of the philosophy of nature were denounced by Cuvier, and

[1] See F. A. Bather: *Fossils and Life.* Pres. Addr. Sect. C. Brit. Assoc. Reports 1920 and cf. W. B. Crow: *Phylogeny and the Natural System.* Journal Genetics 1926, p. 144, footnote 1.

have fallen out of modern zoology. Cuvier's scheme of four independent divisions of the animal kingdom was opposed to a general homology. With the advent of evolutionary ideas the animal kingdom was again considered as a related whole, and according to Haeckel the whole of the multicellular animals could be traced back to the single type of the gastraea from an evolutionary point of view. This, however, is a conclusion from embryology, adult animals not being considered as comparable.

Homology of the Embryo.

The discovery of embryological homology by Haeckel was an important step forward in the history of morphology, but it introduced no new principle or method. If the adult body of the organism of any given species must be compared with that of another, so also the life cycles, of which those bodies each form one stage, would be expected to show a parallelism with one another. And this is readily seen to be the case. Not only is the fertilized egg homologous in two vertebrate species, but the successive products of that egg, as it grows to form the embryo, are successively equivalent. The precise homology of each successive stage must, of course, be settled by detailed morphological analysis, but the fact that an embryological series exists, beginning with the egg, repeated in the development of each generation, must itself show the general existence of homologies of the life cycle. If adult animals are comparable with one another, and

also the eggs from which they arise, there can be no doubt as to the homology in the intervening stages. Haeckel pointed out certain detailed homologies of these intermediate stages (*blastula*, *gastrula* . . .), the earlier ones of which are not difficult to trace throughout the wide series of the animal kingdom. Somewhat similar are the embryonic and juvenile stages of some plants (*protonema*, *proembryo*, etc.). The existence of these homologies strengthens the general comparison of life-cycles, but if they were not visible, the equivalence of life histories would remain based on the equivalence of the end-points (egg and adult).

Although it is hardly conceivable that the egg of organisms seen to be alike as adults could pass through their stages of development in a totally different manner, yet a somewhat similar difficulty arises from the fact that there is some dispute as to which stages in different species should be compared with one another. Early in the history of embryology it became obvious that the embryo in the higher types is comparable with the adult in some of the lower groups.[1] Thus, for

[1] That embryonic development is from the homogeneous to the heterogeneous was recognized by Harvey in his *Generation of Animals*, 1651. In 1797 Autenrieth compared the series of embryonic stages in the individual with the animal series as a whole. Oken (1809-11) in dealing with the seriation of the animal kingdom noted that members of each class pass through preceding classes during development. Animals he regarded as equivalent to various embryonic stages of man. Tiedemann, in 1808, and J. F. Meckel (1808-1812) also pointed out the parallelism of embryonic stages with lower animal classes, and the topic was fully dealt with by E. Serres (1824-1826), E. Geoffroy St. Hilaire (1822, 1833), von Baer (1834) and many subsequent authors. In later years it received an evolutionary interpretation. Von Baer stated that the evolution of species is essentially of the same nature as individual development. It became the basis of Haeckel's biogenetic law: that the development of the individual repeats that of the

example, the land vertebrate in its embryonic stage possesses certain characters (e.g., gills or parts of gills), which are found in the adult fish, but are not present in the mature stage of the land vertebrate. In spite of its very great differences the tadpole is more strictly comparable with an adult fish than the frog is. And among invertebrates if the attempt be made to compare the highly developed insect with the lower invertebrate types, not adapted to an aerial environment and without high specialization of the nervous system, surely it is more legitimate to take the caterpillar rather than the imago as the unit of comparison.

Homology among Parts of the Same Individual.

Unity of plan implies a general agreement in the structure and arrangement of parts of the whole individual in different species. Similarity between species extends to varying degrees. Often the individual parts of related species are closely similar, and show strict homology by their whole organization as by their details of construction. In the same way the life history itself may show homology, as well as the individual stages thereof. The life history is an extension of the individual in time, just as the body is an extension of it merely in its spatial aspects. The body is subsidiary to the life-history, of which it is only one phase. The life history, it need hardly be mentioned, can be divided up by the recognition of definite

race. Haeckel made the important distinction between *palingenetic* characters, to which this law applies, and *coenogenetic* characters which are not repetitive, in his *Anthropogenie* 1874.

crises or turning points.[1] The body is thus only one unit in the series of the life history. It remains essentially uniform only for part of the time and then gives place to another phase, differing considerably in organization. In the same way there are units composing the body, and it is possible to detect homology among them. Everyone is familiar with the duplication of parts of the body (*bilateral homology*, *homotypy*, e.g., right and left arm) or the repetition of certain parts (*serial homology*, *homodynamy*, e.g., fingers, teeth, vertebræ, leaves of plants). These parts are not exactly alike, and yet they exhibit a similarity in plan and organization, often very close, so that they are undoubtedly homologous.

Many controversies have centred upon the question of the homologies of the embryonic stages. In opposition to the attempt to compare them with adult stages in other species considered therefore as lower, it has been urged that embryonic stages differ in certain respects from all adult forms (e.g., in lacking the high sexual differentiation). Hence it has been said that adult forms only should be compared. But the two points of view : (i) comparison of adult of one form with embryo of " higher " type, and (ii) comparison of adults of different types are by no means mutually

[1] Invagination of the blastosphere, formation of coelom, appearance of gill slits, etc., or in post-natal periods by other changes, such as change of teeth, puberity, etc. In many animals the stages in the life history are clearly marked out as in the insects. Many have a larval stage, the transition from which is well marked. Birth itself is only one stage of development, and differs in oviparous and viviparous animals. All organisms have such definite stages, if not always equally obvious. In plants there is the period of germination following the resting stage in the seed.

exclusive. In fact, the one implies the other when it is remembered that the embryo of a species is homologous with the adult of the same species.

This leads to some features of the problem of homology which can only appear as paradoxes to those who consider it from a purely causal point of view. The whole cannot be equal to its parts, yet the individual (the organic whole) can and must be homologous with its parts. This principle is easy to see on developmental grounds, but it was recognized, apart from its special evolutionary application, by Goethe.

Thus the kind of equivalence which is spoken of as homology is certainly not the *equality* of mathematics. Nevertheless there is, in mathematics, an equivalence which is spoken of as homology and is recognized by mathematical intuition, as for example, in geometry, where a triangle may be divided up into parts which may have similar properties to the whole. Nevertheless the homology of the mathematicians is not biological homology, since it is rather the equivalence of ideal constructions than of sense experiences or images built upon the latter.

The ordinary case of homology, as between adult individuals of different species might be expected to be reduced in its simplest terms as the proposition

$$a : b = c : d$$

It is necessary to have two terms to represent each individual, for a totally undifferentiated mass could show no homology. Now because of meristic homology their relation expressed $a : b$ really comprises a number

of subsidiary relations, $a^1 : b^1$, $a^2 : b^2$, $a^3 : b^3$ . . . And these in their turn must be really analysed into others. The life history consists of phases, each phase is a body consisting of serially homologous parts. Each part, however, is subdivided into other parts (e.g., the two halves of a vertebra, the two halves of a leaf) which are homologous. And in the actual analysis of organisms various stages can be detected. Haeckel[1] was led to postulate six stages of individuality, the simplest unit being the cell. But the cell is not the limit of morphological analysis and the tracing of homology is only limited in practice by the technical means at our disposal (microscopy, microtomy, micro-dissection). And there is no means of deciding, in thought, where the line is to be drawn. Hence the reduction of the homological relation to the *mathematical* proposition

$$a : b = c - d$$

is an artificial device. But we have seen that thought is not necessarily artificial and it follows that homology is not a causal concept, but an imaginative construction, and in mathematics can only be compared with the process of idealization.[2]

Homology and Analogy.

Hence it comes about that authors, taking homology in a limited and quantitative sense, have been unable to sharply define its limits, and controversies as on the

[1] Haeckel: *Gen. Morph.*

[2] See A. Wolf. *Introduction to Scientific Method.* London, 1925.

distinction between homology and analogy have arisen. We have seen that, early in the history of morphology, this distinction did not exist. Then it was brought in by Owen, but subsequently authors tried to make other distinctions. These distinctions are based on certain assumptions as to evolutionary descent which will be examined subsequently. For the moment we will remark that, whilst there are many cases in which it is not easy to decide whether we are dealing with homology or analogy, there are an infinitely greater number which no competent observer would have any hesitation in placing as one or other category of resemblance. As has been stated, the decision must be made on actual anatomical comparison, by the agency of an imaginative apprehension, which cannot be replaced by any quantitative scheme.

SYMMETRY AND PROPORTION

Symmetry as Inter-relationship.

In the section on Individuality, it was shown that this quality is imposed upon the organism in virtue of its compound nature. The individual is made up of cells, organs, segments of varying orders, and sometimes having an evident colonial structure. By the diversity of these units and their arrangement in various ways the individual peculiarities are expressed. There is also an inter-relationship of parts both in time and space. This is partly recognized in time as the causal relation of successive stages of development in the theory of epigenesis, partly as teleological relationship which, in an anthropomorphic manner, expresses this relation as the aims and objects of development. In space the inter-relationship of parts is well seen in correlation. This is very fully established in all organisms and was used by Darwin as an explanation of the persistence of certain characters which are not in themselves favoured in natural selection.

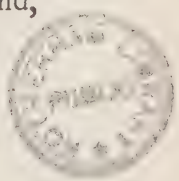
This inter-relation of parts, except for its purely causal, physico-chemical aspect, which is the field of experimental morphology[1] (experimental cytology,

[1] C. Davenport: *Experimental Morphology* (New York and London, 1896, reprinted 1899, 1908), although not including recent work is certainly one of the most synthetic and therefore valuable treatises on this subject.

embryology and much that is classed as physiology if looked at from the comparative point of view) is most readily studied in definite form in the problem of symmetry. That organic bodies are more or less symmetrical must have been noticed by everyone, but it is so commonplace a fact that it has often been ignored. Yet as we hope to show, few topics offer such abundance of concrete data for morphological investigation, and the possibility of expression in mathematical form suggests a treatment comparable with that of inorganic objects.

Organic and Inorganic Symmetry.

It is instructive, in view of what has been said on theory and hypothesis, to compare the symmetry in minerals and organisms. Few organic objects approach the apparently absolutely regular forms of crystals. Symmetry in the living is often apparently an approximation to mathematical form, and often quite obviously only a very rough approximation. Unquestionably such plant structures as flowers and fruits and even the leafy branches of the plant, but especially the bodies of animals, including our own, present a certain degree of symmetry. In some natural objects it is very pronounced so that apparently mathematically perfect forms, comparable with the shapes of crystals occur in organic nature. Examples are found in birds' eggs and in the shells of many microscopic organisms (especially Radiolaria and Diatoms). But the forms of minerals are fewer, and,



as I have had occasion to point out elsewhere,[1] differ in the fact that they are simpler, involving figures bounded by plane surfaces only, whereas those of organisms, in relation to their colloidal constitution, are based on the sphere.[2] Contrast, in relation to this, the scientific treatment of crystal form with that of symmetry in organisms. Crystallography, or as it has been called by one of its exponents[3] *the morphology of crystals*, is an exact science. The classes of crystals are limited in number and defined upon a mathematical basis. Moreover the forms can be explained in a physico-chemical (molecular) manner, just as any other physical phenomena are. No comparable treatment of the symmetry of organisms has yet been elaborated. It is, theoretically, not impossible to treat organisms in exactly the same way as crystals, and many relations have been worked out between the forms of organisms and the properties of their colloidal constituents.[4] A mathematical treatment is to some extent artificial when it is applied to any set of sense data, as would appear from what has previously been said. Nevertheless the mathematical treatment is much less legitimate in dealing with organic objects, unless supplemented with hypothesis, than in dealing with crystals, for the following reasons. A crystal is

[1] *Symmetry in Organisms.* Amer. Naturalist, 1928. Consult this article for an account of the subject giving some of its details which would be out of place in a general methodological treatment.

[2] Crow : *loc. cit.*

[3] N. Story-Maskelyne : *Crystallography, a treatise on the Morphology of Crystals.* Oxford, 1895.

[4] See on this aspect of the subject especially D'Arcy W. Thompson, *Growth and Form*, London, 1917.

very nearly mathematically perfect and one single mathematical figure expresses its structure, without any strain upon the imagination. On the other hand, as I showed by examples in a previous work[1] a single organic structure may come under different geometrical constructions according to the way it is considered. Very much in the same way as we must abstract certain characters of the organism in order to trace its phylogeny, so we can only deal with isolated aspects of the structure as geometrical figures. This is not a difficulty that is strictly confined to organisms. Even crystals show it to some extent, but the problem does not become acute in the inorganic. It arises from the fact that most organic structures only approximate to known geometrical forms, and in living things it is possible to find a number of equal approximations. Thus the human body as such cannot be mathematically expressed. In many ways it forms an excellent example of bilateral symmetry but might, if some of its internal organs were alone concerned, come under the category of the laterally differentiated. Crystals do not present such numerous possibilities, and hence difficulties, of mathematical classification. But even the crystal is not mathematically perfect.[2]

Although the mathematical treatment of living things is thus subject to the limitations which we have been led to expect from a consideration of the possibilities of theory and hypothesis in general, yet within this limit

[1] *Symm. in Organisms, loc. cit.*

[2] For details, see *loc. cit.*

the method is an exceptionally valuable one. That a geometrical treatment of organic morphology is in any way possible shows that the inter-relationship of the parts of organisms is a definite and concrete relation, which will be more acceptable on this account to those trained in the physical sciences than perhaps another relation with which morphology has to deal.

In short, the mathematical treatment of organic form has lagged behind that of crystals and the inorganic in general (e.g., forms of waves) not only because organisms present a greater diversity, variety and, above all, complexity of form, making the subject more difficult to develop, but also because the geometrical archetypes do not bear such a close relation to the sensory impressions of the organic world as they do to the mineral. A crystal does not conform to more than one geometrical pattern with any degree of exactness. The organism, on the other hand, although it undoubtedly does agree in a very real way with various geometrical figures, cannot be altogether subsumed under one mathematical construction only. Rather there are several figures which have a legitimate claim to *represent* the organic body, although they do not agree with any one exactly. In other words, resemblance but not identity with mathematical formulations is the rule in the organic realm.[1]

From the earliest times artists have known of various numerical proportions between the dimensions of

[1] *Complete* identity is not expressed even in crystals, but they are much closer than geometrical.

different parts of the human body.[1] Various *canons of proportion* have been proposed as standards whereby the length of one part could be ascertained by a knowledge of the others. Those who have given the closest attention to nature have realized that such a canon is neither an exact measure of inter-relationship on the one hand, nor an altogether artificial contrivance on the other.

A canon of proportion was in use amongst the ancient Hindus, Egyptians, Greeks and Romans. In the Middle Ages it was known wherever art flourished, many indications of it being traced among the great artists of Italy. The scheme, for example, was well known to Leonardo da Vinci, Raphael and Michael Angelo. In Holland it claimed the attention of Hubert and Jan Van Eyck[2] ; later of Rubens, Van Dyck and Rembrandt. Albrecht Dürer in German, dealt with the subject in two works, and considered it very important both from a practical and a theoretical point of view. During the last two centuries, various proportional relationships have been noted by artists and naturalists.

The simplest of these canons of proportion indicate a relationship between the length of the body and one of its parts, e.g., the length of the face, the cubit.[3] Others are concerned with the relation-

[1] For an account of these, as well as modern views, and a critical comparison, see Bertram C. A. Windle : *The Proportions of the Human Body*. London, 1892.

[2] See Windle *loc. cit.* (espec. p. 48 for table of authors who have dealt with the subject and for references).

[3] The length from the elbow to the end of the middle finger, formerly used as a unit of measurement.

ships of part to part, one of which is considered as a standard, as in the modulus of Carus[1] which was the length of the human spine at birth (atlas to last lumbar vertebra), i.e., one-third of the length of the adult human spine. Allied to these are the angular measurements which have sometimes been used, as the facial angle of Camper.[2]

These rules of proportion do not hold good with a high degree of exactness. The stature cannot be calculated with accuracy from a knowledge of the length of the face, for instance, yet given the length of face it can be said that the stature will fall within certain limits. The proportional relationship is thus assimilable to the relation of causality which fixes the one condition, within certain limits and provided no other factor intervenes, from the existence of another. As, however, time differentiation does not enter into the simpler proportional relationships, they are not spoken of as causal.

These geometrical relationships among parts hold good for varying ranges of experience. Some vary from race to race, some from species to species. Others are peculiar to types which do not coincide with divisions of the natural system but which are nevertheless real.[3] But the simpler proportional relationships, such as those dealt with in connection with the human frame by artists, are only sporadic examples of a

[1] *Die Proportions-Lehre der Menschlichen Gestalt*, 1854.
[2] For a short account of this, and mention of other authors, see E. Miriam Léon: *Anatomy for the Art Student*, The Physiologist, 1925.
[3] See section on relationship and type.

phenomenon which is profoundly impressed upon matter in general and which is exhibited in a particular way in the world of the organic. This general symmetry of natural objects has already been referred to.[1] Haeckel attempted to found a complete system for the description of organic objects, but subsequent writers have not pursued it with any success, as the nature of the problem has not been realized and the subject therefore regarded as artificial,[2] owing to the very large obvious difference between the natural objects and the geometrical forms supposed to represent them.

Another difficulty lies in the kind of symmetry relationship observed. Although some of these are very simple yet many need complex mathematical treatment. Many natural objects are asymmetrical. Of course the terms symmetry and asymmetry are relative. An ellipse is asymmetrical with regard to a circle and so on. But it is found that many organic objects involve the use of higher powers in their formulation than do inorganic objects. Thus whereas crystal growth involves the addition of an equal balancing mass (i.e., a fully formed crystal has the form of a cube, etc.) the growth of a plant takes place very frequently in a manner that involves a logarithmic proportion (e.g., the Fibonacci series of leaf arrangement). It is impossible without an immense amount of technical detail to do justice to this conception,[3] but

[1] See also Crow: *Symmetry, loc cit.*

[2] I have attempted to show (*loc. cit.*) some of the ways in which the subject has been and might further be developed.

[3] See, however, Crow: *Symmetry, loc. cit.*

the preponderance of spiral formations in nature is well known.[1] To be precise, the spiral is a closer approximation to the forms of organic growth than are other curves, e.g., the ellipse. Moreover, several different spiral curves exist and the logarithmic spiral and the proportions (the Fibonacci series) on which it is founded are more correct representations than the Archimedean spiral of the ordinary geometrical series.[2] This agrees not only with the spiral curves shown by the leaf arrangements in plants and the shells of molluscs, but the proportions of many natural objects are represented by the numerical series corresponding with it rather than with simple geometrical relations. The so-called "Golden Mean" defined as the point of division of a line such that the ratio of the lesser to the greater part is equal to the ratio of the greater to the whole, is nothing but the provision of three lengths equal to the first three members of the series.[3] This proportion is widespread in nature,[4] whilst the higher Fibonacci numbers are common in formulations of leaf arrangements.

The mathematical analysis of natural objects into segments of length, area and so on is based on their

[1] See T. A. Cook: *The Curves of Life, being an account of Spiral Formations and their Application to Growth in Nature, to Science and to Art, with special reference to the manuscripts of Leonardo da Vinci.* London, 1914. And for a modern view of leaf arrangement: A. H. Church: *On the Interpretation of the Phenomena of Phyllotaxis,* Oxford, 1920.

[2] Recently a still more complex series, the so-called Phi series has been found to give closer results in some cases. It has been chiefly applied to objects of art, see below.

[3] Or more closely, the Phi series.

[4] See e.g., Zeising: *Lehre von der Proportionen,* 1854.

differentiation, making it possible for example to measure from one point of a body that can be definitely fixed as the standard. It need hardly be pointed out that the points chosen are, therefore, not arbitrary, but supplied by nature. Nevertheless, it is possible to take innumerable different ratios. Some of these provide very simple arithmetical proportions, others are more complicated in mathematical expression, whilst still others have defied analysis altogether. The reality of these relations, however, cannot be questioned and they cannot be regarded as artificial on the grounds that the selection of the points of measurement are chosen by the investigator. The method of their selection rests upon the ability to find those relations which show the closest approximation to mathematical standards, but the relations are inherent in natural objects themselves.

But not only natural objects can be subjected to this analysis. Objects of art have been treated in this way. Of course some art productions show natural proportions because they are consciously copied from nature. Thus one expects figures of the human form to comply with the canons of proportion, and artists have usually constructed them in this fashion, although they may have deviated therefrom for the purpose of producing special effects.

But in many works of art there is an entirely free artistic creative activity, as in the grouping of objects in a picture, for example. This kind of grouping can be analysed in the same manner as has been applied

to natural constructions. Some attempts of this kind have been made, with surprising results. The logarithmic spiral, for instance, or some related curve, has been projected on to a picture. It is found[1] that the lines of the curve mark out important and specially emphasized points or divisions of the representation much in the same way that the spirals of living things mark out areas of growth or deposition of some kind. Thus it appears that, as previously stated, the object of art has a rhythm or structure which in some cases approximates to a mathematical expression. It is not claimed, of course, that beauty can be reduced to mathematical formulæ, for like the organism the object of art is full of departures from the mathematical. Nevertheless art productions have a recognizably rhythmic construction and this is most obvious of course in music,[2] where it can also be related to mathematics. Goethe claimed that art is a continuation of the activity of nature, hence he thought a morphology of objects of art to be a possibility. The comparative study of art-products opens a wide field which may perhaps one day be brought into relationship with the morphology of organisms. The present condition of science is, however, scarcely favourable to the development of such an extended synthesis.

[1] See Cooke, *loc. cit.*
[2] cf. application to poetry in appendix to work of Cooke, *loc. cit.*

CLASSIFICATION AND TYPE

The earliest ideas which were formed as to organic relationship can be ascertained from the study of the first systems of classification. It is clear from an examination of these that animals and plants were originally classified in the same manner as other objects were and still are—namely, according to certain points of resemblance and difference found to be conveniently ascertained in their examination. The present system of biological classification on the other hand, whilst still involving, as does all classification, the use of resemblances and differences, chooses what are regarded as natural resemblances, indicating what is known as affinity and what is considered to be due to blood relationship.

Several points thus present themselves for consideration. In the first place, what is the criterion of a natural resemblance, what constitutes affinity, and does the latter necessarily indicate community of descent?

It is well known that the classification of non-living objects must be based upon a certain system if the classification is to be of any value. Thus elements are grouped according to their atomic weights, whilst planets are classified according to their position in the solar system. The grouping of planets according to weights, or of elements according to distribution in

nature has no known meaning, whereas if they are arranged on the other basis it is found that a certain order is established. If elements are arranged in order of their atomic weights they are also *ipso facto* found to be arranged according to a number of other properties. The *periodic system* so obtained is thus really an arrangement of the elements according to the sum of a number of characters displayed by each element. The periodic system is thus based on a number of different properties, the use of the atomic weight being taken as the guide[1] because it is the simplest way of ascertaining the place of the element in the system and was first used to build up the system. Prout's hypothesis, which was the predecessor of Mendeléef's periodic law, was much ridiculed when first proposed, because this agreement of the atomic weights with other properties was not realized, and the whole system seemed arbitrary. When the correlation of atomic weight and other properties had been fully demonstrated by Mendeléef and later workers, the existence of a certain rhythm in connection with the series of atomic weight could no longer be denied and even prophecies of new elements could be made.

Although the peculiarities of living organisms may prevent a quantitative system, such as the periodic law of chemistry, from being applied to the classification of animals and plants, yet the natural system which is gradually evolving as morphology

[1] More recently another property, atomic number, has been found even more valuable as a key to the periodic relations of the elements.

develops, is no mere arbitrary arrangement based on convenience. Every practical worker on plant or animal classification in museum, herbarium or the field, knows that the natural system is frequently very inconvenient. It would be much easier to assign the plants or animals to their place in some purely artificial scheme, like the old Linnean system. The term natural system is, therefore, a justifiable one, although what is so called may only represent an approach to the ideal. Nevertheless much progress in attaining this system has been made in the history of the subject.

The very earliest systems of classification, certain characters such as weight and physical properties played practically no part in the arrangement of organisms. This was because these properties were not an important constituent in the sense experience of living organisms, i.e., the observation of them. Others such as size, shape and colour were more obvious and were at first used. It was soon recognized, however, that neither the size nor colour were important, because resemblances and differences between these qualities were not found to be correlated with other resemblances and differences. On the other hand, form resemblances were found to be correlated in a most remarkable way, so that soon whole systems of form relationships could be worked out.

The stature and habit of plants were the chief means of subdividing the vegetable kingdom in the systems of Aristotle and Theophrastus, and similar arrangements

are met with in the mediæval herbals[1]. The division of the larger plants into trees, shrubs and herbs is a legitimate one as far as the characters of size and shape are concerned, and it is of interest that this classification of external forms of vegetation has in modern times been developed in the service of plant geography,[2] without any conception of natural affinity, but proving that a differentiation of a system of classification based on such characters is possible. The division of plants into *Herbae* and *Arbores* persisted in the classification of J. Ray (1704), and was followed by other artificial systems, based on examination of parts of the flower. The best known of these was the celebrated Linnean system, in which the primary position of the plant was determined by counting the number of stamens. As explained elsewhere,[3] these systems arose in the attempt to find a key-character, i.e., a single means of distinction which would enable one to bring together plants alike in all their features, without the detailed examination of the latter. Just as from the first some obvious characters, e.g., colour, had not been found to be connected with the general organization of plants, so the external form and size of vegetation were abandoned, although not so readily, as to some extent *habitus* is apparently connected with other features. The arrangement of the floral parts, however, was soon found to be unsatisfactory from the same point of view

[1] cf. Crow : *Phylogeny and the Natural System*, Journ. Genetics, 1926.
[2] First suggested by Humbolt in his *Cosmos* (1844-49) this system has been developed by Drude (*Die Oekologie der Pflanzen*, Braunschweig, 1913).
[3] Crow, *loc. cit.*

and the artificiality of his system was recognized by Linnaeus himself, who even put forward some suggestions as to the natural affinities of certain groups, although hesitating to found a complete natural system.[1]

The earliest systems of animal classification, like those of plants, were based on certain selected characters. In fact, animal classification may be said to have developed more rapidly than that of plants, inasmuch as external characters never played an important part. Even Aristotle avoided placing whales with fishes, and although at the beginning of the modern period some use was made of superficial appearances, yet this stage in the history of the subject was soon passed over. In the works of Linnaeus, use was made of the presence and absence of key characters in the definition of groups, but he was unable to find any one set of organs which could be used for classification throughout the animal kingdom, and consequently a larger number of characters were referred to, in defining the larger groups of animals, than in plants.

Although the unsatisfactory character of systems of classification has been remarked by nearly all systematists, the latter have never lost faith in the fundamental basis of their pursuits. This depends upon the fact that one can say that, with regard to any particular

[1] In his *Philosophia Botanica* Linnaeus makes some remarks on the principles of classification which show that he did not regard systematic arrangement as an arbitrary procedure. In reality, the distinction between an artificial system and a natural one is a fallacious one. Every system produced by the human mind is a natural product, but every system is artificial in its applications. Cf. remark of Goethe, quoted later.

character a given species is related to another. The resemblance in any particular feature is perceived, and is a natural phenomenon, having as much claim to reality as the structure of a single species. The description of a single organic structure involves comparison, just as much as does the account of relation of two species. To say a leaf is more flattened in one part than in another is not of a different category than the statement that one leaf is flatter than another. The natural system is thus the description of nature just as the morphology of the individual is an account of a natural object.

The system, however, involves something more than description. Very frequently it is found that when one species resembles another with regard to a given character, it also resembles it with regard to a second and different character. Thus poultry as well as sparrows have feathers, they both also lay eggs. Hence the possibility, in fact, the inevitability of the natural system. This is true over a very wide field, and is so very firmly established in thousands of cases that it would be idle to question the aims of classification. Nevertheless it must not be taken as implying the universality of correlation between any two or more particulars that happen to be found associated, even if they occur together in a number of cases. All systems have their anomalies, and it would be a mistake to suppose the characters of the organism fit into a uniform scheme. As Goethe says, the natural system is a contradiction in terms, nature knows no system. Thus

we find animals like *Ornithorhynchus* and *Echidna* which lay eggs but which do *not* have feathers. To insist upon a scheme which would be applicable to the whole organism instead of to its separate characters would be to ignore the very basis of individuality.

Nevertheless, the world of organisms does not present a completely haphazard distribution of characters. This is proved by correlation in the manner above indicated. The natural system of relationships is, therefore, and has been in its most primitive, crude and admittedly artificial progenitors, an interconnected regulated scheme comparable, for instance, with the periodic system of the elements or Bode's law of the position of the planets. Just as these laws are not perfect and are only approximate, capable of replacement by other formulations, but never to be completely destroyed, so the natural system is based on an impregnable condition in nature, which lends itself to progressively differentiated formulations which appear in the history of the subject as successive systems of classification.

This condition of natural relationships, expressed in a simple manner in the artificial system of classification of which the Linnean is the type, is also visualized by those conceptions of a *scala naturae* which have also appeared among philosophico-biological writings from time to time. Strictly the scale of natural objects depends on a somewhat different principle to the grouping of species into families and orders. But in the formulation of most authors the two are closely

intermingled. This principle depends on the simple quantitative variation of any particular character. Thus if in a given species a given character has a given value x, then in another species it may have the value $x + m$. But in a third species the value of the character may be $x + m + n$. To be applied, however, the character must be homologous in each case. However, we have seen that there are varying degrees of homology and the older authors constructed series upon characters which must now be distinguished as analogous. Thus Bonnet[1] regarded flying fishes as intermediate between fishes and birds. On the other hand a good modern example of the principle is seen in the seriation in the degree of development, duration during life and number, of the gills of Vertebrata, a progressive reduction of which is witnessed in higher forms.

The principle can also be applied to the graduation or seriation in the possession of a number of characters. Thus birds possess both oviparity and feathers, most mammals are viviparous and are devoid of feathers. *Ornithorhynchus* and *Echidna*, however, are animals which show oviparity, but are without feathers. They are therefore, from the point of view of these characters, intermediate between birds and the majority of mammals. The gradual loss of aquatic characters in the higher animals and plants may be looked upon from the same point of view.

In a former publication[2] the author made a critical

[1] *Contemplations de la Nature*, 2 vols. Geneva, 1764.
[2] Crow *Phylogeny*, *loc. cit.*

study of such a series in colonial algae, which happen to have a varying number of cells in the colony. In algae many such series can be established. In mosses and ferns the gradual sterilization of the reproductive area of the plant has formed the thesis of Bower's *Origin of a Land Flora*. Floral morphology is rich in series, generally interpreted as indicating reduction in the gradual evolution of the flower and its specialization in relation to the visits of insects. That the series exist involves no hypothesis, it is a simple fact of observation. Equally plain are the examples from the animal kingdom. Segmented invertebrates present excellent examples of series in which the members of the series, i.e., the different species, can be arranged not only in order of their number of segments, but in progression in the complexity of the individual segments. In vertebrates the series of the teeth[1] is well-known and has formed the theme of many discussions of evolution. Whatever view is held as to the direction of evolution, the series themselves are undeniable facts. Many other series will be found described in the work of Cope.[2] The grouping of species into successive subdivisions, viz., *class*, *order*, *family*, *genus* and *species* depends upon a principle which is equally important in classification as are the aforementioned principles of *correlation* and *seriation*. Characters may show seriation throughout a number of species, or only the generic or group characters may be

[1] See Osborn: *Evolution of Mammalian Molar Teeth*. New York, 1907.
[2] E. D. Cope. *The Primary Factors of Organic Evolution*, Chicago, 1904.

considered as forming a sequence. The occurrence in a number of species of more than one common character indicates relationship of these species and if a large number of characters are held in common they are placed in the same group. But groups are of different categories. Individuals are not all alike, but early in the history of biology it was recognized that groups of individuals similar in such a degree that a general description of any one would serve without modification for all the rest, existed in nature, generally propagated amongst themselves, and produced offspring to which the same description could be applied as to the parents. This group is the so-called *species*, a term taken over from the scholastic philosophy. It will be unnecessary to enter into the attempts that have been made, from time to time, to define the species, except to point out that although it seems to defy analysis it cannot therefore be dismissed as a convention. Like the individual, the species is somewhat elusive when one attempts to grapple with its limits. Species unquestionably grade into one another sometimes,[1] just as they are sometimes isolated by natural lacunae.[2] Moreover species may be subdivided into microspecies as our knowledge

[1] For evidence of the extreme degree of intergrading of species in lower forms of life, see Crow, *The Taxonomy and Variation of the Genus Microcystis in Ceylon.* New Phytologist, 1923. *Variation and Species in Cyanophyceae.* Journ. Genetics, 1924. *Abnormal Forms of Gonium.* Ann. and Mag. Nat. Hist. 1927. *Contributions to the Morphology of Colonial Cyanophyceae* Archiv. f. Protistenk 1928. On the principle of fair samples, we must assume, at least for the organisms of the kind studied, that intergrades are characteristic of these groups.

[2] For examples of discontinuity of species, see Bateson: *Materials for the Study of Variation, treated with especial regard to Discontinuity in Evolution.* London, 1894.

of them progresses, and most of the units known as species at the present day are far smaller subdivisions than those recognized, say, in the time of Linnaeus. In a very clear manner the species increase with our greater powers of description. This does not mean a species is merely a verbal description. A species is a collection of individuals each of which bears an aggregate of characters, which may be described verbally ; the characters, however, exist apart from the description and form part of nature. In this sense the species is a reality.

The groups into which species may be grouped, even in the most artificial system, are not altogether arbitrary. Even in those systems in which the primary divisions depended upon a single key character the latter was not chosen at random. On the other hand the character chosen, even in the systems depending on external form, was something suggested by the observation of nature. One might, for example, have classified plants according to their specific gravity, but nothing in nature suggested a classification of this kind, and it has never been carried out. The first systems of classification were therefore only relatively artificial.

As classification advanced it became clear that relationships inherent in animals and plants reveal themselves to the observer. Consequently the idea of key-characters was given up.

But even in the Linnean system the definition of the groups depended upon the distribution of characters in nature. Thus for example the main division into

warm-blooded and cold-blooded animals was chosen not because the temperature of the blood has any special priority in the determination of animal structure, but because it was found that these were two characters which did not vary throughout very large numbers of animals. Again mammals are characterized, as their name implied, by the fact that they suckle their young. This *a priori* has no special value, but it is found to be constant throughout a group which in other respects forms a series, or rather a system of series. Body-form on the other hand is extremely variable. Not only so, but some characters often apparently insignificant were correlated throughout large groups, e.g., feathers and ovipary.

The hierarchical construction of the natural system, i.e., its constitution from successively larger groups, viz., *genera*, *families*, *orders* and *classes* is simply the expression of the distribution of characters in nature. Some features, like the presence of a backbone, happen to be distributed throughout large groups of species, others like the ruminant stomach are confined to smaller assemblages.

The term character, as it is used in systematic biology, does not, however, apply to the fixed and static. The backbone, it is true, is found throughout the group of the *Vertebrata*, but it is not identical in any two species, still less in divergent members of the larger groups. The characters of the vertebrates, or of any other group, are rather of the nature of archetypes, i.e., units that remain homologous, but not identical.

Hence it is that larger groups may sometimes be defined by their tendencies rather than by definite characters. This does not destroy the essentially concrete nature of the definition, since it is based on the perception of nature quite as well as the observation of the individual is.

The system of Cuvier[1] represented a transition from the relatively artificial Linnean system to the modern conception. In it the presence and absence of simple characters were abandoned as far as concerned the great groups, which were based upon the general arrangement of the circulatory and nervous systems. Here the animal kingdom fell into four great subdivisions—*Radiata*, *Mollusca*, *Articulata* and *Vertebrata*. The characters of each were thus, as Von Baer[2] pointed out, based on the symmetry of the parts. Thus the articulate animals, as well as the vertebrates, possess a nervous system, but they were not regarded by Cuvier as equivalent because of their different orientation within the body. Whatever view is taken of the relation of articulate animals to vertebrates, however, it is agreed that the latter exhibit a uniformity of plan amongst themselves, and this unity of plan, involving homology of the different organs and systems, is a more valuable criterion of relationship than the presence or absence of any individual character could be, since it is found to extend over large groups and enables large series of organisms to be brought into

[1] *Le Règne Animal*, 4 vols. Paris, 1817.
[2] *Ueber Entwickelungs geschichte der Thiere. Beobachtung und Reflexion.* Königsberg, 1828.

a harmonious scheme. Linnaeus himself, as has been mentioned, knew of the advantages of this method, and his attempts towards a natural system were based on what he called the simple symmetry of all the parts. Modern classification is entirely based upon the examination of the whole organization, in fact upon morphology, and the definition of groups usually calls for something more than the mere recital of simple characters. The use of embryonic characters was introduced by Von Baer[1] in 1828, who also urged the importance of symmetry. R. Leuckart,[2] H. Milne Edwards,[3] Huxley[4] and Haeckel[5] are chief amongst those who established the use of the whole organization of the organism, as a criterion of its systematic relationship. Nevertheless the method of classification is fundamentally unchanged, since it depends upon the distribution of the characters in nature, although it is now known that the arrangement, inter-relationships and development of the parts are more important than the more superficial and simple characters. The latter are sometimes found to characterize large classes, as in the example mentioned above, but more frequently morphological interpretation is a necessity in the determination of systematic position.

We are now in a position to answer two of the questions with which we opened our consideration

[1] *loc. cit.*

[2] *Die Morphologie und die Verwandschaftsverhältnisse der wirbellosen Thiere. Brunswick,* 1848.

[3] *Cours elementaire d'Histoire Naturelle.* Paris, 1855.

[4] *Introduction to the Classification of Animals.* London, 1869.

[5] *loc. cit.* (*Gen. Morph.*)

of relationship. To the question as to the criterion of a natural resemblance it must be said that *a priori* there is no resemblance that is more " natural " than any other. Nevertheless some resemblances bring together organisms which are alike in other respects. Sometimes a group selected for one character shows another in common. This is only a special case of homology. The latter condition can only hold good between two differentiated systems, which may be artificially represented $a : b$ and $a^1 : b^1$. The parts of an organ or system that is homologous with any other organ are themselves inter-related in fundamentally the same manner as are two correlated characters. Natural resemblance, although arrived at in a different realm of investigation, by workers on the description of species, is therefore nothing else than a form of homology, and in latter years morphology has been consciously applied to the solution of problems of relationship. This, however, was not the case in the early history of the subject. No knowledge of homology as a concept directed the first efforts in the classification of organisms. Yet we have seen that these efforts were not at random, and the characters used in classification were not arbitrary. In other words relationships were perceived in nature, and any subsequent rationalization of their selection is altogether secondary and took place at a later date.

In answer to the question as to what constitutes affinity it must be indicated, as I have had occasion to point out elsewhere,[1] that affinity was distinguished

[1] See Journ. Genetics, 1926.

from mere similarity early in the history of classification. Linnaeus made the distinction and it was emphatically expressed by P. Agardh[1] in 1825. On the other hand homology and analogy were not distinguished by anatomists until 1843, when Owen made use of these terms. Both the conception of affinity and of homology are historically older than that of evolution. Affinity is, therefore, not the application of an evolutionary idea to a phenomenon of nature. On the other hand, the use of the terms affinity and relationship by Agardh and other earlier writers is a remarkable prevision of subsequent interpretation. Like many other symbolical terms it has proved, upon analysis, that a real similarity exists between the affinity of plants and animals, expressed in the natural system, and the affinity between individuals, seen in human relationships. This equivalence of the relationship of organisms with the relationship by descent of human individuals, must be considered in the subsequent section.

Principle of Types.

Before leaving the consideration of the natural system, however, reference may be made to the *principle of types*. The term type is not uncommonly used in biology and frequently serves to indicate a selected individual or species, a description of which will serve as a model for the whole group. In systematic botany or zoology the type specimen is the original

[1] See *loc cit.*

individual, upon the description of which the species is based. This use of type specimens is based upon the uniformity of the species. In biological education the type system, due to Huxley, is still of importance. It is based upon the selection of a species to represent a group. In the description of a species in this way differentiation must be made between those characters which are peculiar to the species and those that are illustrative of the group.

This conception of a type is, therefore, an artificial one, since—because of its specific peculiarities—no particular animal can fully represent the group. A natural basis for the principle of types is, however, afforded by the primitive type of Goethe, the archetype of Owen. Each group has its own primitive type, which is, however, never equivalent to any particular species. It is nevertheless absolutely concrete, since it is that element which is common to all the species of a group, and can be perceived in the structure of them all. Of course it can be abstracted, by analysis, from the specific elements, and in this sense is an abstraction. As Goethe himself pointed out, it is not a purely ideal construction but is something equally given by nature, as built up ideally in the human mind. For Goethe and his school, the distinction between deductive and inductive science had no meaning. From the point of view of modern inductive science, however, it may be said that the archetype is a perception.

Each subdivision of the natural system is, according

to the modern evolutionist view, descended from a common ancestor. The evolutionary interpretation of classification is to be dealt with subsequently, but it will be seen at once that the primitive type of Goethe, or as it may be conveniently distinguished, the archetype, is not the supposed common ancestor. The latter, if we are to take it at its face value, in the naïve evolutionary terminology commonly employed, was an actual species that existed sometimes in the past history of the earth at a definite time and place. The archetype on the other hand is not a species, but it exists here and now within the various species. The latter, however, represents an ancestral form and the best way of obtaining a picture of the former inhabitants of the earth is by the study of the archetypes of the living. It is found that fossils have their specific peculiarities and only conform in part with the supposed characters of ancestors. The reason for this will become clear when we have compared the natural system with a genealogical tree.

As systems of classification are diverse, so also will be the systems of types. If the supposed natural system is taken as a basis one may speak of the *vertebrate type*, the *arthropod type*, and so on. Within the vertebrates one can distinguish a *reptilian type*, an *avian type*, a *mammalian type* amongst others. These types are distinguished by a large number of characters ; a knowledge of each involves the study of a large number of anatomical characters and their transformations. But it is equally legitimate from the point of method,

to speak of an *aquatic type*, a *terrestrial type*, an *aerial type*, and so on. Provided it is known upon what basis the classification is made, any system may be used. In the terms given as examples it is clear that the environment is the determining factor. From a physiological point of view, we may distinguish *holozoic*, *holophytic*, *saprophytic*, *parasitic* types, and so on. Even in dealing with anatomical characters one may confine attention to certain features only. Thus anthropologists speak of *dolicocephalic* and *brachycephalic* types (based on the dimensions of the head) which may be classed in various natural groups, because the characters upon which they are based are associated with other characters (e.g., hair colour), which may vary indefinitely. Psychologists also distinguish human types based on mentality and behaviour, and the latter may not altogether be correlated with racial characteristics. All these methods are legitimate in themselves provided their limited basis is recognized. In each case the type must not be confused with the individual unit (*individual*, *species*, *genus*) in which it is expressed. An individual may be classed as dolicocephalic because he has certain head dimensions, but the dolicocephalic type only exists in virtue of a number of individuals having these dimensions. In simple cases like this, where only one character is used, the method of types approaches the statistical method.

RELATIONSHIP BY DESCENT

Analogy of Natural System with Genealogical Table.

The natural system has undergone many modifications, and on many important questions as to its constitution authors are not agreed. Yet that it has a foundation in nature has been shown from a consideration of the distribution of characters. That it must be partly artificial follows from the infinite diversity of natural objects, which make it necessary for the observer to limit his choice of the means of classification. The system may assume many different forms, but any of these that express the relationships of organisms may be spoken of as natural. Before the belief in evolution became general amongst biologists, the classification of organisms was expressed in different forms. Sometimes, by confining attention to a limited set of characters, the organic world, or a part thereof, was arranged in the form of an unbroken sequence. This view was chiefly favoured by philosophical writers who could grasp elusive analogies and neglect observed distinctions. Most biologists, to whom the differences were plainer than the resemblances, found it difficult to represent the relationship in this manner and preferred the simple manner of presenting affinities in the form of a reticulum or network.[1]

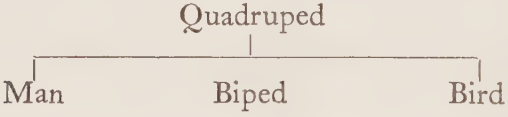
[1] Definitely portrayed by V. Donati: *Storia naturale marina dell' Adriatica.* Venice, 1750. The zoologist P. S. Pallas represented the system in the form of a polyhedron (*Elenchus Zoophytorum*, 1766).

But as the seriation of natural objects could not be denied ; as for example the embryonic series, the palæontological series, the geographical series, and the numerous systematic-anatomical series such as those leading to vestigial organs were revealed, the idea of seriation could not be avoided and a compromise was made ; the natural system became represented in the form of a genealogical tree. This, in brief, is the history of evolution.

There are some authors who profess a belief in evolution, but who claim to be sceptical as to the representation of evolutionary history by the series of the natural system. Their evolutionary belief must then be based on faith alone, since it is precisely these natural sequences, whether embryonic, palæontological, geographical or systematic, and their natural basis homology, that afford the evidence that evolution has taken place. Homology, seriation and affinity were explained by Darwin and other early evolutionists, by comparing them with the relationship which exists between individuals having a common descent, as in a human fraternity. This is the fundamental basis of evolution, quite apart from any theory or hypothesis as to the method by which it has taken place, as by natural selection, inheritance of acquired characters, mutation, and so on.

The majority of the forms under which the natural system has been represented present an undeniable resemblance to a genealogical tree. The latter presents the seriation so characteristic of living things, in the

tabulation of one generation after another. It also has the advantage of showing in its most typical form, not a single series but a ramifying system. Now this is just what is required to represent the natural system. To take a very simple example. The majority of land vertebrates have a quadrupedal form : their axis is horizontal and they are supported on the earth by four feet. Man has an upright posture and is supported only on his two lower extremities which are obviously homologous with the hind limbs of horizontal vertebrates. Birds are also bipeds, and have more or less attained an upright position. But because of their other characteristics (e.g., presence of feathers) birds cannot be associated with man in the same group. If then one wishes to construct a diagram of the natural relationship of man and birds to quadrupeds (leaving the latter unanalysed for the moment) one can put forward the following scheme :



This, as far as it goes, is a perfectly correct representation of the facts. Of course comparative anatomists have proceeded such an enormous distance beyond a simple scheme of this kind that very many other characters must be taken into account in the modern systems of classification, and even at an early stage, the quadrupeds were known to fall into a number of classes.

The natural system also assumes the form of a genetic series in a somewhat different manner. The successive subordination of groups, the species being a subdivision of the genus, the genus of the family, and so on, is no doubt an arrangement which is necessary to meet the exigencies of classification. But it is not an altogether artificial scheme. As has already been pointed out, but as it is necessary to repeat in view of the common misapprehension of the natural system, the characters are themselves perceived to have a certain distribution and do not appear haphazardly. This is most readily seen in a single individual where the arrangement of the parts can be observed simultaneously, but under special conditions it can be seen in a group of individuals which form part of a system. And there is no distinction of method between the construction of part of the system and that of the whole. An observer at a given time can only perceive part of the system, but the system as a whole is nevertheless based on perception. A great many conceptual factors enter into the construction of any special system, but unless a system is in opposition to sensory experience it must be regarded as natural. There is no completely natural system, but all systems based on sense experience are natural up to a certain point. Now in most systems the arrangement is hierarchical, i.e., there are successive divisions of species, genus, family, order and class. These systems can thus be arranged in the form of a branched system comparable with the genealogical tree. This

arrangement, therefore, represents the natural distribution of characters.

It seems possible to find in this arrangement something more than a superficial analogy with the genealogical tree. The generic characters are older than the specific, those of the family than those of the genus, and so on. It is assumed that characters change in the course of evolution, each new species being represented as the offspring of a preceding species. There are certain difficulties in making this comparison, however. Although a system of classification represents nature, it is only one way of representing it. And hence there are not one, but many ways of representing it. Hence there are, and have been, many different systems of classification. There are certain general agreements between systems of classification, resting on the nature of the organisms. Even supposed conventional methods have arisen largely from the nature of the material. But the infinite diversity of characters, even in the simplest organisms, renders the task of classification always an incomplete one. Take for instance the bacteria. When these organisms were discovered nothing seemed simpler than to classify them into half a dozen species based on microscopic appearance. Later staining reactions, cultural methods and investigations of life history opened out innumerable possibilities in the classification of bacteria. The introduction of anatomical characters in the classification of animals by J. Ray (1628-1705) was a great step forward in the history of zoology. Modern

embryological and even cytological research is resulting in great changes in classification, especially of the invertebrates, and cytological consideration now dominates the system of classification of algae and fungi.

Classification is therefore always changing and in many cases two or more alternate systems are equally possible. This has been pointed out with clearness by the Japanese botanist, Bunzo Hayata,[1] who has proposed a new system called the dynamic, and has applied it to the flowering plants. The principle of this system is that species, genera and families occupy a varying position according to the characters considered.

The present systems of classification are limited by the qualities which are at present at our disposal as a means of classification. No one who has followed the history of classification can suppose that the present systems have any more or less permanent value than the systems that preceded them. Like all other contemporary thought they represent merely a section of a continuously developing interplay of ideas.

If this is so, what effect will it have on the supposed analogy of the natural system and the genealogical tree? It cannot destroy the analogy, of course, that is firmly established by actual comparison. But it must be remembered that what we are comparing is not the organism as a whole, but its characters as individual items. In speaking of human genealogy one speaks

[1] *The Natural Classification of Plants according to the Dynamic System.* Reprinted from the *Icones Plantarum Formosanarum.* Taihoku and Tokyo, 1921.

in terms of individuals. The actual descent is traced and can be described in any particular instance.

Consider the relationship of father and son. Everyone knows that in bodily characteristics the two individuals are often closely similar. Sometimes this similarity extends to minute details, not only of the bodily organization, but to capabilities and habits. This similarity is explained as being due to heredity, provided it cannot be shown to be impressed upon the two individuals from a similar environment. But the father is only one of the parents, and in human heredity, as in other instances, one must consider inheritance from the mother as well as from the father. The son, in most cases, resembles the parents far more closely than he does other individuals. But the best example of hereditary resemblance in man is undoubtedly that seen in identical twins. It is well known that human pairs of twins are of two kinds, namely those in which the members of the pair happen to be born together, but which have developed from separate fertilized ova, and those in which the pair spring from a single fertilized ovum which has divided into two. The latter are generally so closely similar that they cannot be distinguished by their relatives, except by artificial means. The extent to which their life is similar is remarkable, similar events sometimes happening at the same time to both independently.[1] In bodily form they unquestionably resemble one another in minute

[1] Consult, for illustrations of this, Galton's *Inquiry into Human Faculty*. London, 1883, reprinted 1907, 1911.

detail. This is typical inherited resemblance, since the two individuals are undoubtedly equipped with the same hereditary material, whatever this may be.

Analysis of Hereditary Resemblance.

The resemblance between identical twins and between two other children of the same parents is of the same nature, it only differs in degree. It is fundamentally due to the same causes, namely, common origin. In the one case the common stock from which the two individuals arise is the fertilized ovum. In the other, the common stem-cells occur farther back in the life history of each parent, but all the reproductive cells (spermatozoa) produced by the male parent originate from a common parent cell, all the reproductive cells (ova) by the female parent likewise, have a common origin in a single unit. Brothers and sisters differ because, as has been definitely proved in numerous cases of Mendelian inheritance and can be seen microscopically in some cases,[1] the reproductive cells of a single individual are not necessarily all alike. But the resemblances are much greater than the differences and in the majority of cases no difference between the reproductive cells of an individual can be detected.

Hereditary resemblance is thus, in the two examples taken, due to common origin, and can be traced from one *cell generation* to the next. There is no need for any hypothesis or analogy in this explanation. Each

[1] The difference of sex of the offspring has been shown in some cases to be correlated with the presence and absence of additional chromosomes.

step can be observed and in some cases has been actually traced by embryologists. The hereditary resemblances between brothers is thus due to the fact that their body is continuous in descent with, and derived from cells that originally formed part of a single cell mass and owed their separate existence to cell division. Human heredity is thus, fundamentally, not different from the simple cases of heredity among lower organisms, especially those consisting of a single cell (*Protista*) which reproduce by fission. Hereditary resemblance in the latter is largely a matter of retaining the parental structure by the two offspring units, but even here, because no organism is a homogeneous mass, it also involves a reconstruction.

Let us assume a homogeneous mass

a a a a

to divide into two equal parts. These may be represented as

a a and *a a*

These may grow by adding similar particles *a* and divide again. Consider however a symmetrical differentiated mass capable of equal division represented in its simplest form by

a b a b

The result of binary fission will be

a b *a b*

If, however, the mass is asymmetrical it can be represented

a b c d

the products of division being

ab *cd*

To restore each of these to the parental form it must add on parts heterogeneous to itself. Thus *ab* must add on *cd*, *cd* must add *ab*. But such adding on of different material is only a form of differentiation which is characteristic of all living matter (probably related to the colloidal constitution of the latter as opposed to the crystalloidal structure of the inorganic world). It may be noted that the last formula will apply to all forms of reproduction if it be taken that one-half, e.g., *ab* represents the soma and thus does does not itself divide, whilst the other half may abstrict a further section to form the soma of the next generation after fusing with another cell produced in the same way. This is the ordinary diagram of the continuity of the germ plasm.

Even in the ordinary conception of heredity it is admitted that, owing to the sexual manner of reproduction, the characters of the offspring are inherited from two different sources, the father and the other. But the latter are themselves alike in a general way, i.e. they belong to the same species or genus, a point to be remembered when one compares the descent of species with the genealogy of individuals. Mating in animals nearly always takes place between individuals of the same species. Crossing is debarred between distantly related species by difference in instincts, structural incompatibility, or in plants, chemical antagonism.[1] Thus the two parents possess a structure

[1] *Foreign* pollen (i.e., pollen of a different species) placed on the stigma of a plant is destroyed in some cases, and nearly always fails to germinate notwithstanding it can generally be germinated artificially in sugar solution.

that is homologous. They may differ in considerable detail, as in the structure of the sex organs themselves. Nevertheless, the resemblance between the sexes, together with its characteristic difference, may be taken as a model of homology. But there are many other cases of homology which have a claim to equal reality. We have seen that unity of bodily type extends at least over the largest divisions (*phyla*) of the natural system and some structural unity (e.g., division into cells) may pervade the whole organic world. Homology is thus a much wider thing than the resemblance of parents to offspring, of parents to one another, or of other individual inter-relationships. Nevertheless, it is assumed that homology in general indicates community of descent, as was indicated by Darwin,[1] and clearly expressed by Haeckel[2] and Gegenbaur,[3] who used it as a means of tracing the descent of species, a branch of morphology to which Haeckel gave the name of *phylogeny*. Gegenbaur[4] specifically stated that the phyletic relationship is established in any particular case in proportion to our knowledge of homology in that instance. This is accepted by many biologists.

The use of homology as a measure of genetic relationship has not, however, been allowed to pass without adverse criticism. The typical opinions of those who believe homology to have another basis than common descent have been put forward by O.

[1] *Origin of Species*. London, 1859.
[2] *Generelle Morphologie*. Berlin, 1866.
[3] *Grundriss der vergleichenden Anatomie*. Leipzig, 2nd ed., 1878.
[4] *loc. cit.*

Hertwig.[1] This author does not deny the existence of homology as deduced from anatomical comparison, but although an evolutionist, he does not think that homology always indicates community of descent. How then does he explain homology in those cases where common origin is not postulated ? He thinks it may be due to the similarity of the laws governing the evolution of animals. These views suggest the possibility of a confusion of homology and analogy, and even of a lack of a real distinction between the two. In all the examples hitherto given there can be no dispute as to the difference between homology and analogy. But homology and analogy may be of different kinds, and in some cases it may be difficult to distinguish between them. St. George Mivart has enumerated over twenty different kinds of what he considers homology, some of which are analogies according to the following account.

That common factors, working in a similar environment, can produce similar forms is not disputed. Analogy in its biological sense is explained in this way. The wings of insects, bats and birds have all developed in relation to the adaptation of the organism to an aerial mode of life, just as, to return to the comparison of evolution with individual descent, the father and the son may both have well-developed arm muscles because they both follow the trade of blacksmith. But the

[1] *Ueber die Stellung der vergleichenden Entwickelungslehre zur vergleichenden Anatomie, zur Systematik und Descendenz Theorie* (*Handb. vergl. exper. Entwickelungslehre der Wirbeltiere* Bd. 3), Jena, 1906, and *Allgemeine Biologie*, 3rd Ed. Jena, 1909.

similarities which are classed as homology are not of this kind. Is it possible that even resemblances of organization can be produced independently in evolution, just as the muscles of the blacksmith or physical culturist may be acquired by individuals taking up these pursuits? In the latter case, however, the character in question, i.e., large muscles, cannot be developed equally by all individuals. Each has his hereditary limitations. And although physical culture shows that great changes may be made by almost any individual who follows certain exercises, it must be remembered that all human beings start with a certain equipment of, for example, muscular tissue. The effect of environment, of exercise, or education is, as has frequently been pointed out, merely to act upon what is already present. Or rather one should say that it is impossible in nature to separate the individual from the environment. The latter is an altogether artificial concept and is equally to be considered as determined by the individual and his heredity, as being the determiner of the individual. According to ordinary terminology the individual is selected by the environment, but it is equally correct to say that the individual selects his environment. Those that select the unfavourable may be exterminated by natural selection.

If with Hertwig one considers homology as due to the similar action of laws of structure and development one can only say that the similar action means that there is some element which has been passed on in evolution

to that particular group which has also manifested itself in another group. The difficulty of conceiving this as a form of relation by descent can only come about when a too narrow view of genetic relationship is held ; when in fact the genealogical tree is confused with the phylogenetic one.

What is meant by the assertion that two distinct species are related by common descent is something different from the supposition that two human brothers resemble one another because they inherit something from their father. The situation is similar in the two cases, but not identical. To go back to the ancestral form of two species, however closely related, would, in general, require many thousands of generations. Now, each individual has two parents, four grandparents and so on. In fifty generations back this number of ancestors exceeds a million million. It is clear that *phylogeny*, that branch of morphology which traces organic descent, has nothing whatever to do with this sort of genealogy of individuals. As I have said elsewhere : " Phylogeny deals with the origin and succession of characters, not with their distribution among individuals."[1] Thus it comes about that a species may have inherited one character from one source, another from another and so on. This is still quite analogous with the situation in which the individual finds itself. The modern researches in Mendelism show that an individual may resemble a grandparent or an uncle rather than one of its parents.

[1] *Phylogeny and the Natural System.* Journ. Genetics, 1926.

Even in the case of simple bi-parental inheritance at least the *two* parents must be considered.

There is, therefore, no need to suppose that all characters are handed down from one generation to the next in unbroken sequence. Still less are we disposed to admit that the peculiar constellation of characters which constitute the individuality is continuous in heredity. Rather we should suppose that it will be repeated at certain rhythmic intervals, according to the so-called laws of chance.